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Standard and routine metabolic rates of juvenile sandbar sharks (*Carcharhinus plumbeus*), including the effects of body mass and acute temperature change*

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Abstract—Standard and routine metabolic rates (SMRs and RMRs, respectively) of juvenile sandbar sharks (*Carcharhinus plumbeus*) were measured over a range of body sizes (n=34) and temperatures normally associated with western Atlantic coastal nursery areas. The mean SMR Q_{10} (increase in metabolic rate with temperature) was 2.9 ±0.2. Heart rate decreased with increasing body mass but increased with temperature at a Q_{10} of 1.8–2.2. Self-paired measures of SMR and RMR were obtained for 15 individuals. Routine metabolic rate averaged 1.8 ±0.1 times the SMR and was not correlated with body mass. Assuming the maximum metabolic rate of sandbar sharks is 1.8–2.75 times the SMR (as is observed in other elasmobranch species), sandbar sharks are using between 34% and 100% of their metabolic scope just to sustain their routine continuous activity. This limitation may help to explain their slow individual and population growth rates, as well as the slow recoveries from overfishing of many shark stocks worldwide.

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Shark populations continue to suffer from overfishing throughout the Northwest Atlantic and worldwide (Baum et al., 2003). The sandbar shark (*Carcharhinus plumbeus*) can serve as a model for overfished coastal shark species, many of which share ecological and ecophysiological characteristics. After the rapid expansion of the Atlantic coastal commercial shark fishery in the mid-1980s, sandbar shark numbers declined 66% by 1991 (Musick et al., 1993; Sminkey and Musick, 1995). Like many of their K-selected relatives, sandbar sharks grow slowly and mature after a minimum of 13–15 years (Casey and Natanson, 1992; Sminkey and Musick, 1995). Demographic models of these species predict very slow rates of population increase even in the absence of fishing pressure, and elasticity analyses of these models demonstrate that the juvenile stage is the most critical life history stage (Sminkey and Musick, 1996; Cortes, 1999; Brewster-Geisz and Miller, 2000). It is necessary, therefore, to understand the actual and potential contributions of various juvenile nursery areas to recovery of the Northwest Atlantic sandbar shark population and to recovery of other coastal shark stocks (Branstetter, 1990).

Bioenergetics models can be used to assess the impacts and requirements of juvenile sharks as apex predators. Metabolic rate is the largest and most variable component of the energy budget for active fish species, and it is critical that it be determined accurately in order to construct realistic bioenergetics models (Ney, 1993). Systematic metabolic rate data for elasmobranchs are only rarely available, and previous models of sandbar shark bioenergetics have relied upon metabolic rate data from unrelated species (Medved et al., 1988; Stillwell and Kohler, 1993).

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The lower Chesapeake Bay, Mid-Atlantic Bight, and adjacent coastal lagoon systems serve as the primary summer nurseries for sandbar sharks in the Northwest Atlantic (Musick et al., 1993). Juvenile sandbar sharks return for four to ten years to these nursery grounds, where they enjoy the benefits of generally high food availability and limited exposure to large shark predators (Musick and Colvocoresses, 1986; Grubbs et al., in press). Juvenile sandbar sharks in the nurseries are exposed to seasonal water temperature variations, as well as shorter time-scale fluctuations associated with their vertical movements and day to day variation. The minimum seasonal temperatures (≈15°C) occur in mid or late May, whereas the maximum temperatures (≈28°C) are reached in surface waters in July and August (Merson and Pratt, 2001). Throughout the day, sandbar sharks perform frequent vertical excursions and thus experience surface and bottom water temperatures that can differ by up to 5°C (Grubbs, 2001). Similarly, in Virginia's Eastern Shore lagoons, juvenile sandbar sharks venture onto broad, warm tidal flats at high tide and return to deeper, cooler channels as the tide recedes (Conrath[1]).

To improve bioenergetics models and to define critical habitat and the current suitability of nursery areas more accurately, standard (SMR) and routine metabolic rates (RMR) of juvenile sandbar sharks were measured over a relevant range of body masses (≈1 to 10 kg) and temperatures (18–28°C) (Merson and Pratt, 2001). This is the first direct measurement of SMR, and the first comparison of paired SMR and RMR, in a continuously active carcharhiniform species.

Materials and methods

All experiments were conducted at the Virginia Institute of Marine Science Eastern Shore Laboratory from June through September 2002. Sandbar sharks (57–124 cm total length; 1.025–10.355 kg) were captured by using hook and line from the surrounding tidal lagoon system and maintained in shoreside tanks (temperature 22–29°C, salinity 34–36‰). Individuals were fasted for at least 48 hours prior to use in an experiment to reduce any confounding effects of specific dynamic action (Medved, 1985).

Standard metabolic rates

Because sandbar sharks are continuously active obligate ram ventilators, SMR measurements were obtained from chemically immobilized and artificially ventilated animals maintained in flow-through, sealed box respirometers (Brill, 1979, 1987; Leonard et al., 1999). Respirometers were constructed of 0.85 cm thick acrylic, sized to accommodate the fish being studied, and covered with black plastic to minimize visual disturbance. Aerated and filtered seawater from a constant pressure head tank passed through the mouth and over the gills of the sharks, was mixed in the chamber by a small recirculating pump, and exited the respirometer by a hose mounted at the top. Water leaving the respirometer was collected, re-aerated, and mixed with a small amount of fresh filtered seawater to help maintain a constant temperature. Turnover rate for the system was 20–30%/hour (Steffensen, 1989).

Sharks were netted, injected with 0.4–1.8 mg/kg of the neuromuscular blocking agent pancuronium bromide through the caudal vein, and returned to the holding tank until they were unable to swim (typically 1–2 min). They were then placed supine on a moist towel and ventilated with aerated seawater while electrocardiogram (EKG) wire leads were inserted subcutaneously over the pectoral girdle to monitor heart rate. Individuals were also given an intramuscular injection (0.2–1.2 mg/kg) of steroid anesthetic Saffan® (alphaxalone and alphadolone; Pitman-Moore, Uxbridge, UK) (Oswald, 1978). Two 20-gauge hypodermic needles were inserted into the dorsal musculature and used to administer supplementary doses of pancuronium bromide and Saffan® whenever any slight tail movement was observed.

The partial pressure of oxygen (PO_2, mm Hg) in the seawater was measured with a polarographic oxygen electrode (Radiometer A/S, Copenhagen, Denmark) mounted in a water-jacketed cuvette (maintained at the experimental temperature) and connected to a digital oxygen meter (Cameron Instruments Company, Port Aransas, TX). All equipment was calibrated to manufacturer's specifications. Oxygen level in the inflow water was measured hourly, and outflow water was otherwise monitored continuously. Water temperature, PO_2, and heart rate were recorded every 10 seconds with a computerized data acquisition system (Daqbook 120 with a DBK52 thermocouple expansion card; Iotech, Inc., Cleveland, OH). The inflow ventilation volume (V_g, L/min) was adjusted to keep oxygen extraction between 10% and 20%. Measured PO_2 values were converted to oxygen content (mg O_2/L) following Richards (1965) and Dejours (1975). Standard metabolic rate (mg O_2/h) was calculated by using the Fick principle (Steffensen, 1989). Because the effects of pancuronium bromide were not reversible, at the end of each experiment individuals were euthanized with a massive overdose of sodium pentobarbital injected into the caudal vein. Sex was then determined and they were weighed to the nearest five grams and measured (precaudal and total lengths).

Standard metabolic rate data for each individual were plotted against time and averaged over all hours (range 1–7 hours) after the outflowing PO_2 stabilized. Standard metabolic rate measurements were obtained at 24 ±1°C on 33 of the 34 animals. In addition, 18 animals were exposed to acute temperature changes (to 18 ±1°C or 28 ±1°C, or to both). Temperature change rates averaged 4.5 ±0.6°C per hour and 6.4 ±1.1°C per hour for cooling and heating, respectively, although these were not statistically different (t =–1.46, df=36, P=0.15). Data

[1] Conrath, C. 2004. Personal commun. Virginia Institute of Marine Science. 1208 Greate Road, Gloucester Point, VA 23062.

collection was not resumed until at least one hour after the chamber had equilibrated to the new temperature (Steffensen, 1989). In order to minimize any systematic errors, the direction of temperature change was not always the same. To quantify the effects of acute temperature changes on SMR and heart rate, Q_{10} values were calculated over the temperature ranges 18–24°C, 24–28°C, and 18–28°C by following the methods of Schmidt-Nielsen (1997).

Routine metabolic rates

An annular respirometer (1250 L; diameter 167 cm) was used to measure RMR (Bushnell et al., 1989; Parsons, 1990; Carlson et al., 1999). A cage (diameter 61 cm) was placed in the center to force the sharks to swim around the perimeter of the tank. Water temperature was controlled during an experiment at 24–26°C by adjusting room temperature.

Sharks were transferred to the respirometer and allowed to recover for 30–90 minutes. The tank was sealed and data recording continued until oxygen content was reduced by 15% (≈two hours). The tank water was then re-oxygenated before the next measurement by pumping the seawater through a membrane oxygenator (Medtronics, Inc., Minneapolis, MN) (Steffensen et al., 1984). A complete RMR experiment consisted of one to five iterations of this process.

Oxygen concentration (mg O_2/L) was measured with a YSI 57 oxygen meter by using a YSI 5739 polarographic electrode oxygen-temperature probe (Yellow Spring Instruments, Yellow Spring, OH). Water temperature and oxygen content were recorded at 20-second intervals with a computerized data acquisition system (model PCA-14, Dianachart, Inc., Oak Ridge, NJ). Routine metabolic rates (mg O_2/h) were calculated from the rate of decline in dissolved oxygen (mg O_2/(L×min)) and the volume of the respirometer (Steffensen, 1989). Swimming speeds (in body lengths per second, BL/s) were determined every 15–30 minutes by averaging the time required for the shark to complete three to six laps. To account for the increased costs of swimming in a circular path, recorded RMRs were corrected to straight line estimates (RMR_{sl}) by following the method of Weihs (1981).

Statistical analysis

Routine and standard metabolic rate data at each temperature were fitted to the allometric equation $MR = a \times M^b$ by using nonlinear, iterative Gauss-Newton regression (Brill, 1979, 1987). This technique provides more accurate estimates of the parameters than log-transformed linear regression (Glass, 1969). The likelihood ratio test statistic was used to test for differences in the allometric exponents (b) among temperatures and between SMR and RMR at 24–26°C. Analysis of covariance (ANCOVA) of log-transformed metabolic rate (with log-transformed mass as covariate) was also used to test the equivalence of the exponents (b) in the untransformed allometric equations. Differences in SMR and heart rate among temperatures were evaluated by using ANCOVA. Analysis of covariance with mass as covariate was used to test for differences in mean SMR Q10's and heart rate Q10's among the three temperature ranges. The relationship between the RMR-to-SMR ratio and body mass was assessed with linear least squares regression. Statistical analyses were performed in Statistica 6.1 (StatSoft, Inc., Tulsa, OK) and SAS, version 8.0 (The SAS Institute, Inc., Cary, NC), with $P<0.05$ taken as the limit for significance. All values reported are means ± standard error of the mean.

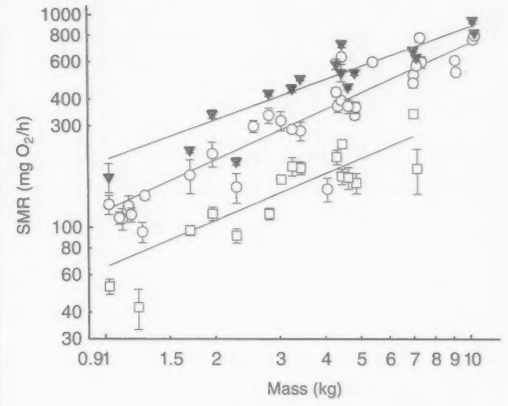

Figure 1

Standard metabolic rates (mg O_2/hr) of juvenile sandbar sharks (*Carcharhinus plumbeus*) as determined by flow-through box respirometry at 18°C (□), 24°C (○), and 28°C (▼). Lines show best-fit allometric equations at each temperature. Error bars indicate ±1 standard error.

Results

Standard metabolic rates

Standard metabolic rate increased with body mass (range 1.025–10.355 kg) at all three temperatures (ANCOVA, logmass, $F_{1,59}=265.04$, $P< 0.001$) (Fig. 1). The best-fitting allometric equations relating SMR (mg O_2/h) to body mass (M, kg) were

$$18°C: SMR = 65\ (\pm 15) \times M^{0.73\ (\pm 0.14)} \qquad n=16,\ r^2=0.71 \qquad (1)$$

$$24°C: SMR = 120\ (\pm 17) \times M^{0.79\ (\pm 0.08)} \qquad n=33,\ r^2=0.84 \qquad (2)$$

$$28°C: SMR = 207\ (\pm 28) \times M^{0.63\ (\pm 0.07)} \qquad n=16,\ r^2=0.87 \qquad (3)$$

Standard metabolic rate increased with temperature for each individual and overall (ANCOVA, temperature,

$F_{2,59}$=20.99, P<0.001). However, the allometric exponents (b) at each temperature were not significantly different (likelihood ratio test, χ^2_2=3.2, P=0.20; ANCOVA, logmass×temperature interaction, $F_{2,59}$=0.81, P=0.45).

The mean SMR Q_{10}'s were 3.2 ±0.4 for 18–24°C (n=14), 2.5 ±0.2 for 24–28°C (n=16), and 2.9 ±0.2 for 18–28°C (n=13). There was no overall effect of body mass on SMR Q_{10}'s (increases in metabolic rate with temperature) (ANCOVA, mass, $F_{1,36}$=0.04, P=0.84), but there was a significant negative correlation between mass and SMR Q_{10} for 24–28°C (P=0.014, r^2=0.36; slope=–0.20 ±0.07). The temperature range did not affect mean SMR Q_{10} (ANCOVA, range, $F_{2,36}$=1.37, P=0.27). The data sets were therefore pooled and the overall mean Q_{10} was 2.9 ±0.2 (n=43).

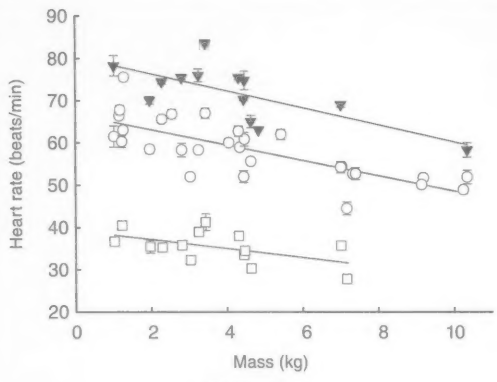

Figure 2

Heart rates (beats/min) of juvenile sandbar sharks (*Carcharhinus plumbeus*) (treated with pancuronium bromide) measured during standard metabolic rate experiments at 18°C (□), 24°C (○), and 28°C (▼). Solid lines represent best-fit linear regressions at each temperature as a function of body mass. Error bars indicate ±1 standard error.

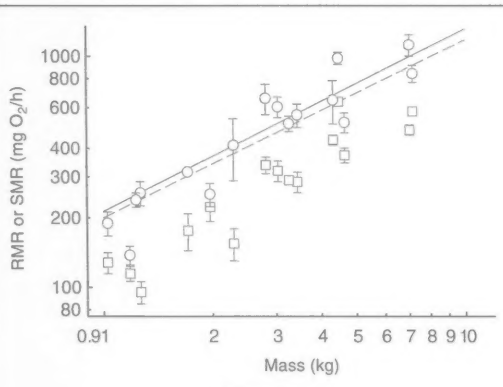

Figure 3

Paired routine (RMR, ○) and standard metabolic rates (SMR, □) (mg O_2/h) of 15 juvenile sandbar sharks (*Carcharhinus plumbeus*) at 24–26°C. Error bars indicate ±1 standard error. The solid line depicts the best-fitting allometric equation with the fish swimming in a curved path in an annular respirometer: RMR = 213 (±38) $M^{0.79(\pm 0.11)}$. The dashed line represents the best-fit allometric equation using the corrected straight-line swimming (RMR_{sl}) estimates: RMR_{sl} = 200 (±33) $M^{0.77\ (\pm 0.11)}$.

Heart rates

Heart rate was negatively correlated with body mass at all temperatures (ANCOVA, mass, $F_{1,50}$=29.99, P<0.001) (Fig. 2). The relationships between heart rate and body mass at each of the three temperatures were

$$18°C: \textit{Heart rate} = 39.3\ (\pm 2.0) - 1.07\ (\pm 0.49) \times M \qquad n=14,\ P=0.05,\ r^2=0.29 \qquad (4)$$

$$24°C: \textit{Heart rate} = 66.7\ (\pm 1.6) - 1.81\ (\pm 0.30) \times M \qquad n=29,\ P<0.001,\ r^2=0.58 \qquad (5)$$

$$28°C: \textit{Heart rate} = 80.4\ (\pm 2.9) - 2.02\ (\pm 0.61) \times M. \qquad n=13,\ P=0.01,\ r^2=0.50 \qquad (6)$$

Heart rate increased with temperature for each individual and overall (ANCOVA, temperature, $F_{2,50}$=64.21, P<0.001) (Fig. 2). However, the influence of body mass on heart rate did not vary among temperatures (ANCOVA, mass×temperature interaction, $F_{2,50}$=0.69, P=0.51).

The mean Q_{10}s for heart rate were 2.2 ±0.05 for 18–24°C (n=14), 1.8 ±0.04 for 24–28°C (n=12), and 2.1 ±0.03 for 18–28°C (n=11). Heart rate Q_{10} was not correlated with body mass (ANCOVA, mass, $F_{1,31}$=0.95, P=0.34). However, an overall significant effect of temperature range on heart rate Q_{10} was observed (ANCOVA, range, $F_{2,31}$= 4.68, P=0.02). 18–24°C and 18–28°C were significantly different from 24–28°C (P<0.001), but not from each other (P=0.08, Tukey unequal n HSD test).

Routine metabolic rates

Routine metabolic rate increased with increasing body mass (Fig. 3). The best-fitting allometric equation relating RMR (mg O_2/h) to mass (range 1.025–7.170 kg) was

$$RMR = 213\ (\pm 38) \times M^{0.79\ (\pm 0.11)}. \qquad n=16\ (53\ \text{trials}),\ r^2=0.82 \qquad (7)$$

The estimated additional costs of swimming in a curved path versus a straight line increased with body mass (range 0.8–19.9%; Fig. 3). With the straight-line swimming (RMR_{sl}) estimates, the allometric equation for RMR became:

$$RMR_{sl} = 200\ (\pm 33) \times M^{0.77\ (\pm 0.11)}. \qquad n=16,\ r^2=0.83 \qquad (8)$$

Although the acclimation periods in the annular respirometer were relatively short, it has been shown that

sandbar sharks recover rapidly from angling stress (6–10 h; Spargo et al.[2]). There was no evidence of systematic decreases in RMR (relating to recovery from handling stress) during individual RMR experiments, which averaged 16.2 ±2.0 hours in length. Using only the final trial for each individual, we fitted RMR to the allometric equation:

$$RMR = 203\ (\pm 35) \times M^{0.76\ (\pm 0.12)}. \quad n = 16,\ r^2 = 0.78 \qquad (9)$$

Routine (average ±SEM) swimming speeds decreased with increasing body size according to the exponential equation speed (bl/s)=3.54 $TL^{-0.43}$ (r^2=0.18) (Fig. 4). In most cases the animal maintained a swimming speed and direction along the outer wall of the chamber for 5–20 minutes before turning around. Because each shark swam at a relatively constant speed, the effect of swimming speed on metabolic rate could not be determined.

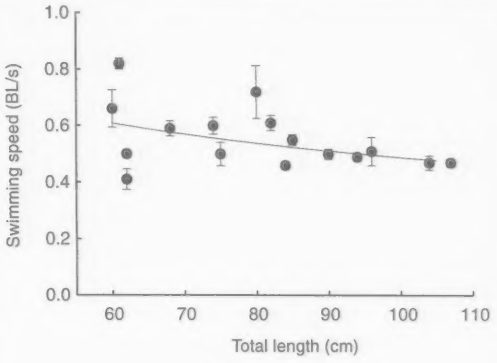

Figure 4

Mean (±1 SE) voluntary swimming speeds of sandbar sharks (*Carcharhinus plumbeus*) during RMR experiments. The solid line represents the best-fit equation: *speed* (*BL*/s) = 3.54×(*total length*)$^{-0.43}$.

Paired standard and routine metabolic rates

Paired SMR and RMR measurements were obtained for 15 sharks (1.025–7.170 kg) (Fig. 3). The mean ratio of RMR to SMR at 24°C was 1.8 ±0.1. The mean ratio of RMR_{sl} to SMR was 1.6 ±0.1. There was no significant correlation between body mass and the ratio of RMR to SMR (P=0.93, r^2<0.01). The allometric exponents for RMR and SMR at 24°C were also not significantly different (likelihood ratio test, χ^2_1=0.002, P=0.96; ANCOVA, logmass×type interaction, $F_{1,45}$=0.33, P=0.57).

Discussion

Effects of body mass and temperature on SMR and RMR

This study presents the first direct measures of SMR and expands the size range over which SMR and RMR have been reported for continuously active shark species (Fig. 5). Sandbar shark metabolic rate, like that of a wide variety of species, increases with increasing body mass according to the allometric equation $MR = aM^b$, with a b of ~0.71–0.79 (Schmidt-Nielsen, 1997). The effects of body mass on SMR, RMR, and RMR_{sl} (b in Eqs. 1–3 and 7–9) in sandbar sharks were similar to published values for other elasmobranchs (e.g., Pritchard et al., 1958; DuPreez et al., 1988; Sims, 1996). The temperature independence of b, previously reported for the lesser sandshark (*Rhinobatos annulatus*) and the bullray (*Myliobatus aquila*) (DuPreez et al., 1988), was evident overall in sandbar sharks. However, there was a significant effect of mass on SMR Q_{10} for the 24–28°C range. These two findings appear to contradict each other, but the 24–28°C pattern may be influenced by small sample sizes at larger body masses (only 2 sharks >7.5 kg).

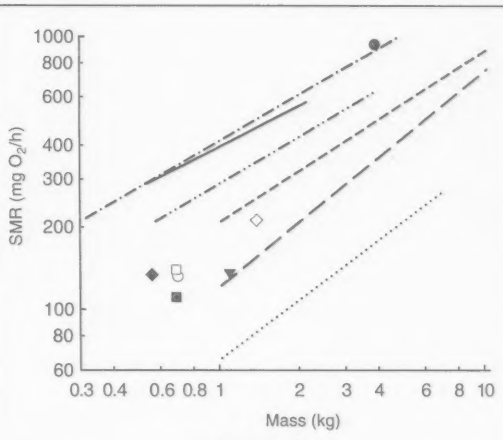

Figure 5

Standard metabolic rates of active elasmobranch species and tunas as a function of body mass: *Isurus oxyrinchus* 18°C (●, Graham et al., 1990); *Sphyrna lewini* 21°C (■), 26°C (○), and 29°C (□) (Lowe, 2001); *Negaprion brevirostris* 22–25°C (▼, Bushnell et al., 1989) and 25°C (◇, Scharold and Gruber, 1991); *Carcharhinus acronotus* 28°C (♦, Carlson et al., 1999); *C. plumbeus* 18°C (·····), 24°C (— — —), and 28°C (– – –) (present study); kawakawa (*Euthynnus affinis*) 25°C (———, Brill, 1987); yellowfin tuna (*Thunnus albacares*) 25°C (– ·· –, Brill, 1987); skipjack tuna (*Katsuwonus pelamis*) 23.5–25.5°C (– · –, Brill, 1979). Lines are best-fit allometric equations at the stated experimental temperatures.

[2] Spargo, A. L., N. Kohler, G. Skomal, and R. Goodwin. 2001. The physiological effects of angling on post-release survivorship in juvenile sandbar sharks (*Carcharhinus plumbeus*). (Abstract.) American Elasmobranch Society 17th Annual Meeting, State College, PA. Website:http://www.flmnh.ufl.edu/fish/organizations/aes/abst2001d.htm [accessed on 26 September 2005.]

The effects of acute temperature change on SMR were consistent with published values for other elasmobranchs (Q_{10}=2–3; e.g., DuPreez et al., 1988; Carlson and Parsons, 1999; Miklos et al., 2003). The Q_{10} for the SMR in elasmobranchs has also been reported to vary with the temperature ranges assessed (Butler and Taylor, 1975; Hopkins and Cech, 1994), but this was not the case for sandbar sharks. It is important to note the distinction between acute temperature changes and seasonal acclimatization when reporting Q_{10} values (Schmidt-Nielsen, 1997). In the present study, sandbar sharks were exposed to rapid temperature changes that mirrored short-term temperature fluctuations experienced in the wild (SMR Q_{10}=2.9 ±0.2). In seasonally acclimatized bonnethead sharks (*Sphyrna tiburo*), the effect of seasonal temperature change on metabolic rate was lower (Q_{10}=2.29–2.39; Carlson and Parsons, 1999).

Cost of activity and routine energy expenditure

The SMR is never realized in fish that must swim continuously to maintain hydrostatic equilibrium or to ventilate their gills. Measurement of SMR and RMR in active species nevertheless allows insight into the division of metabolic costs between swimming and maintenance processes. For example, the average metabolic rate of juvenile scalloped hammerhead sharks (*Sphyrna lewini*) in the wild was 1.4 times the estimated SMR (Lowe, 2002). In sandbar sharks, the RMR to SMR ratio (1.8 ±0.1) and RMR_{sl} to SMR ratio (1.6 ±0.1) were similar to those observed and estimated for several elasmobranch species (e.g., 1.5, Brett and Blackburn, 1978; 1.4, Nixon and Gruber, 1988; 1.7, Carlson et al., 1999). In other words, SMR comprises 56–63% of total metabolic rate at routine activity levels. Because the allometric exponents for RMR and SMR were not different at 24°C, we conclude that the RMR-to-SMR ratio (and, therefore, cost of activity) is also size independent, at least over the size range of sandbar sharks tested.

Our metabolic rate data span the size and temperature ranges relevant to the summer populations of juvenile sandbar sharks in Chesapeake Bay and other western Atlantic nursery areas (Grubbs et al., in press; Merson and Pratt, 2001). Bioenergetics models require estimates of field activity and corresponding energetic costs (Lowe, 2002). The swimming speeds of sandbar sharks in the annular respirometer (mean 0.55 ±0.03 bl/s) were well within the range of activity levels observed in nature (Grubbs, 2001). After the application of an oxycalorific coefficient of 13.6 J/(mg O_2) (Elliott and Davison, 1975), the RMR and RMR_{sl} for a 1-kg sandbar shark at 24°C represent energy expenditures of 69.7 and 63.4 kJ/day, respectively. These values are comparable to those for the lemon shark (*Negaprion brevirostris*, 67.7 kJ/day; Nixon and Gruber, 1988), *S. tiburo* (80.2 kJ/day; Parsons, 1990), and *S. lewini* (96 kJ/day at ~28°C; Lowe, 2002) . The Q_{10} values for SMR obtained between 18° and 28°C demonstrate that juvenile sandbar shark metabolic demands change significantly as ambient temperature changes, both on short time scales and over the course of the summer stay in the nursery areas.

Heart rates

Heart rate decreased with increasing body mass but increased with temperature (Fig. 2), as it does for other ectothermic species (Schmidt-Nielsen, 1997). Heart rates of juvenile sandbar sharks were comparable to heart rates of two other shark species while swimming (Scharold et al., 1989; Scharold and Gruber, 1991), although the sandbar shark data should be interpreted with caution. Pancuronium bromide has been shown to exhibit vagolytic activity in mammals (Melnikov et al., 1999), but to our knowledge its effect on shark heart rates is unknown and would depend on the resting vagal tone. In the dogfish (*Scyliorhinus canicula*), resting vagal tone increased with temperature between 7°C and 17°C (Taylor et al., 1977). The resting vagal tone and resulting elevation in heart rate after treatment with pancuronium bromide could be significant in sandbar sharks, especially at the higher temperatures. If so, Figure 2 may reflect the effect of temperature and body mass on intrinsic heart rate.

Measuring SMR of immobilized sharks

Standard metabolic rate is defined as the oxygen consumption of a postabsorptive-stage fish at rest, and it is considered the minimum metabolic cost of organismal maintenance (Brett and Groves, 1979). Two methods are commonly used to determine SMR. In the first, the slope of a power-performance curve relating the logarithm of oxygen consumption rate to relative swimming speed is extrapolated back to zero activity (e.g., Lowe, 2001). However, extrapolation does not take into account physiological differences between active and quiescent fish, specifically the induction of anaerobic metabolism during high-velocity swimming, and may misrepresent SMR (Brett and Groves, 1979; Cech, 1990). Further, swimming kinematics can be significantly altered in a swim flume, leading to overestimates of SMR (Lowe, 1996, 2001). The second option for measuring SMR is to confine the fish in a sealed or flow-through respirometer (e.g., Brill, 1987; Hopkins and Cech, 1994). This process works well for sedentary species, but active fish will struggle in such situations, requiring the use of paralytic and sedative agents, as well as artificial ventilation.

Several studies have confirmed, however, that the two methods yield identical results (SMRs and allometric exponents) in various fish species (e.g., yellowfin tuna [*Thunnus albacares*]; kawakawa [*Euthynnus affinis*]; skipjack tuna [*Katsuwonus pelamis*]; rainbow trout [*Onchorynchus mykiss*]; American shad [*Alosa sapidissima*]; aholehole [*Kuhlia sandvicensis*] [Brill, 1979, 1987; Dewar and Graham, 1994; Leonard et al., 1999]). Moreover, treatment with anaesthetics has been shown to have no effect on the SMR of little skate (*Raja erinacea*; Hove and Moss, 1997) or nursehound (*Scyliorhinus stellaris*; Baumgarten-Schumann and Piiper, 1968).

Because sandbar sharks are continuously active, we chose to measure SMR in immobilized and artificially ventilated animals in flow-through respirometers. As a check of this technique, a two-point power-performance curve was constructed by using the logarithms of self-paired SMR and RMR and the mean swimming speed of the animal in the annular respirometer. The average slope for 15 sharks (0.38 ±0.04) at 24–26°C was similar to the slopes of power-performance curves for four other ectothermic shark species (0.2, Scharold et al., 1989; 0.34, Scharold and Gruber, 1991; 0.38, Carlson et al., 1999; 0.32, Lowe, 2001), and we interpret these data as additional evidence that the technique provides acceptable results. This approach, moreover, avoids the expense and difficulties of developing a swimming tunnel large enough to accommodate juvenile sandbar sharks and may well be generally applicable for generating power performance curves in other continuously active fish species.

Elasmobranch metabolic rates and the cost of growth

The published SMRs of active elasmobranchs are well below those of high-energy demand teleosts (e.g., the endothermic tunas; Korsmeyer et al., 1996), with the exception of the endothermic mako shark (*Isurus oxyrinchus*) (Graham et al., 1990) (Fig. 5). Brill (1987, 1996) proposed that the high SMRs of tunas are an unavoidable consequence of their morphological, biochemical, and physiological adaptations for extremely high maximum aerobic metabolic rates, specifically that their large gill surface areas have led to high osmoregulatory costs (but see Brill et al., 2001). Most elasmobranchs, including the sandbar shark, have less than one third the gill surface area of a similar-size tuna (Muir and Hughes, 1969; Emery and Szcepanski, 1986). These modest mass-specific gill surface areas and corresponding low rates of oxygen delivery in ectothermic sharks likely dictate slow asymptotic growth rates (Pauly, 1981), in contrast to those of tunas, whose cardiovascular systems are adapted for meeting multiple metabolic demands (including growth) (Bushnell and Brill, 1991; Korsmeyer et al., 1996; Brill and Bushnell, 2001).

Significant levels of specific dynamic action (SDA, the elevation in metabolic rate in conjunction with protein synthesis after a meal [Brown and Cameron, 1991]) can probably not be met by the cardio-respiratory systems of elasmobranchs, particularly in continuously active species such as the sandbar shark, while they sustain routine activity levels. The oxygen consumption rate following a meal can exceed 2–3 times the SMR (DuPreez et al., 1988; Sims and Davies, 1994; Ferry-Graham and Gibb, 2001), whereas the RMR of sandbar sharks was 1.6–1.8 times SMR. Assuming that the maximum metabolic rate is 1.8 to 2.75 times the SMR (Scharold et al., 1989; Lowe, 2001), we determined that sandbar sharks are using between 34% and 100% of their metabolic scope just to sustain routine activity levels.

Given these limitations, sandbar sharks and other active elasmobranchs probably make tradeoffs among metabolic demands at the expense of SDA or growth to remain within their available metabolic scope, or they may adjust their behavior to seek cooler waters during digestion (Matern et al., 2000). Because rapid incorporation of ingested amino acids into body proteins is not possible, many elasmobranchs may have to reduce the rate of digestion or integrate SDA over a longer period (or do both). For example, estimated daily rations for several elasmobranch species average 1–2% of body weight per day (e.g., Bush and Holland, 2002; Dowd et al., 2006), compared to 4% or more in fast growing teleosts (e.g., Olson and Boggs, 1986). Not surprisingly, sandbar sharks in the Northwest Atlantic mature only after 13–15 years and grow less than 10 cm per year during that time (Sminkey and Musick, 1995). Growth rates for many other large, active elasmobranch species are also slow (Branstetter, 1990). Future research might well focus on exploring the relationship between SDA, active metabolic rates, and metabolic scopes of slow growing, continuously active sharks.

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Abstract—Using a bioenergetics model, we estimated daily ration and seasonal prey consumption rates for six age classes of juvenile sandbar sharks *(Carcharhinus plumbeus)* in the lower Chesapeake Bay summer nursery area. The model, incorporating habitat and species-specific data on growth rates, metabolic rate, diet composition, water temperature (range 16.8–27.9°C), and population structure, predicted mean daily rations between 2.17 ±0.03 (age-0) and 1.30 ±0.02 (age-5) % body mass/day. These daily rations are higher than earlier predictions for sandbar sharks but are comparable to those for ecologically similar shark species. The total nursery population of sandbar sharks was predicted to consume ~124,000 kg of prey during their 4.5 month stay in the Chesapeake Bay nursery. The predicted consumption rates support the conclusion that juvenile sandbar sharks exert a lesser top-down effect on the Chesapeake Bay ecosystem than do teleost piscivores and humans.

Estimating consumption rates of juvenile sandbar sharks (*Carcharhinus plumbeus*) in Chesapeake Bay, Virginia, using a bioenergetics model*

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The lower Chesapeake Bay, Mid-Atlantic Bight, and adjacent coastal lagoon systems serve as the primary summer nursery areas for the Northwest Atlantic Ocean sandbar shark (*Carcharhinus plumbeus*) population (Musick et al., 1993). Sandbar sharks are the most abundant large coastal sharks in the Mid-Atlantic Bight (Musick et al., 1993) and an important part of the commercial shark catch. After the rapid expansion of the fishery in the mid 1980s, the sandbar shark population in Virginia's coastal ocean waters declined by approximately 66% by 1991 (Musick et al., 1993). Meanwhile, catch rates in the lower Chesapeake Bay, the core nursery area for juvenile sandbar sharks, remained relatively stable (Musick et al., 1993). Because juvenile sandbar sharks return to the coastal or estuarine nursery grounds for the first four to six summers of life (Sminkey and Musick, 1995; Grubbs et al., in press), these nursery grounds are vital to the life history and potential recovery of the Northwest Atlantic sandbar shark stock (Branstetter, 1990; Hoff and Musick, 1990; Sminkey and Musick, 1996; Cortes, 1999).

Despite the abundance and position of elasmobranchs at the apex of many coastal and pelagic food webs, their energetic demands and the role of elasmobranchs as predators have rarely been quantified (Gruber, 1985; DuPreez et al., 1990; Sundström and Gruber, 1998; Lowe, 2002; Schindler et al., 2002). In the Chesapeake Bay, sandbar sharks occupy an apex position in the food web, preying upon

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Table 1

Parameters, distributions, and values used in error analyses of the sandbar shark (*Carcharhinus plumbeus*) bioenergetics model. See text for parameter definitions. For parameters with triangular distributions, the initial estimates described in the text were assumed to be the most likely values.

Parameter	Distribution type	Mean or most likely value	SE or range	Source
SMRa	Normal	120.0	17.3	Dowd et al. (2006)
SMRb	Normal	0.788	0.076	Dowd et al. (2006)
Q_{10}	Normal	2.89	0.16	Dowd et al. (2006)
ACT	Normal	1.62	0.11	Dowd et al. (2006)
SDA	Triangular	0.10C	0.06–0.17C	DuPreez et al. (1988), Sims and Davies (1994), Duffy (1999), Ferry-Graham and Gibb (2001)
L_∞	Normal	164 cm	16.4[1]	Sminkey and Musick (1995)
t_0	Normal	−3.8 yr	0.38[1]	Sminkey and Musick (1995)
K	Normal	0.089	0.0089[1]	Sminkey and Musick (1995)
p	Normal	0.75	0.075[1]	Sminkey and Musick (1995)
F	Triangular	0.20C	0.17–0.38C	Wetherbee and Gruber (1993)
U	Triangular	0.07C	0.05–0.08C	Brett and Groves (1979), Duffy (1999)

[1] SE was assigned by the authors to yield a coefficient of variation of 10% (*sensu* Bartell et al., 1986)

a number of commercially important species such as menhaden (*Brevoortia tyrannus*), blue crabs (*Callinectes sapidus*), striped bass (*Morone saxatilis*), and bluefish (*Pomatomus saltatrix*) (Medved and Marshall, 1981; Medved et al., 1985; Stillwell and Kohler, 1993; Ellis, 2003). Interestingly, previous ecosystem models have predicted both significant (Stevens et al., 2000) and negligible (Kitchell et al., 2002) top-down effects of changes in shark biomass on ecosystem structure, depending primarily on the trophic complexity of the system and the incidence of omnivory (Bascompte et al., 2005).

Because the sandbar shark is one of the few species for which many of the necessary modeling parameters have been measured, it serves as an excellent system for assessing the bioenergetics and ecosystem role of large coastal elasmobranchs. This article has the following objectives:

1 to construct a realistic bioenergetics model for juvenile sandbar sharks in the Chesapeake Bay summer nursery grounds. Because previous sandbar shark models have suffered from a lack of species-specific data (Medved et al., 1988; Stillwell and Kohler, 1993), we have incorporated updated species-specific and habitat-specific data.
2 to use the model to assess the role of juvenile sandbar sharks as predators in the Chesapeake Bay to aid ecosystem modelers and fishery management efforts.
3 to test the sensitivity of the model to uncertainty in parameter estimates using error analysis to identify future research priorities (Kitchell et al., 1977).

Materials and methods

Study area and nursery habitat

The core sandbar shark nursery area (~500–1000 km^2; Grubbs and Musick, in press) in the lower, eastern Chesapeake Bay supports a seasonal population of ~10,000 individuals (Sminkey, 1994), composed almost entirely of sandbar sharks <90 cm precaudal length (PCL) (Musick et al., 1993; VIMS[1]). Juvenile sandbar sharks move actively throughout the nursery area, covering large activity spaces (>110 km^2) and the entire water column, as shown in telemetry studies (Medved and Marshall, 1983; Grubbs, 2001).

Sandbar sharks in the nursery area are exposed to both long-term and short-term changes in water temperatures. Juvenile sandbar sharks inhabit Chesapeake Bay at seasonal temperatures ranging from 15 to 29°C (VIMS[1]). During the months of July and August, a seasonal thermocline also develops in the lower Chesapeake Bay, which sandbar sharks will cross repeatedly throughout the day (Grubbs, 2001). The magnitude of the temperature gradient from top to bottom is typically 5–6°C (VIMS[1], Chesapeake Bay Program[2]).

[1] VIMS (Virginia Institute of Marine Science) Shark Ecology Program Longline Survey. 1973–2003. Unpubl. data (as a Microsoft Excel file). [Available from J. A. Musick. 1208 Greate Road, Gloucester Point, VA 23062-1346.]

[2] Chesapeake Bay Program Water Quality Database. Website: http://www.chesapeakebay.net/data/index.htm [accessed on March 2003.]

Bioenergetics model

Rates of anabolism, catabolism, and waste losses (Table 1) were used to construct a bioenergetics model that predicted daily energy consumption (C_D, in joules per day, J/d):

$$C_D = RMR_D + SDA + G_D + F + U. \quad (1)$$

The model used a daily time step, consistent with the determination of daily energy ration. Due to the reporting of the daily routine metabolic rate (RMR_D), specific dynamic action (SDA), fecal losses (F), and excretions (U) as fractions of consumption (see below), we rearranged Equation 1 and solved for C_D to yield the model:

$$C_D = \frac{RMR_D + G_D}{(1 - SDA - U - F)}. \quad (2)$$

We set the immigration and emigration dates for the simulation as May 15 and September 30, respectively (VIMS[1]).

We used the model to estimate daily energy ration for average individuals within each of six age-classes using the Chesapeake Bay nursery (Musick et al., 1993). In turn, we combined energetic requirements with diet composition data to estimate rates of food consumption (daily ration) and predatory impact of individual sharks over the course of the summer for each age class. Finally, these individual estimates were merged with estimates of population size and age structure to estimate the overall predatory demand of juvenile sandbar sharks in the Chesapeake Bay nursery area.

Model parameters

Routine metabolic rate (RMR) Like a number of carcharhiniform species, sandbar sharks are continuously active, which leads to high daily metabolic expenditures (e.g., Carlson et al., 1999). As a result, metabolic rate is the largest and most variable component of the energy budget for these active fish (Kerr, 1982; Boisclair and Leggett, 1989). Unfortunately, because of a paucity of available data, metabolic rate parameters are often borrowed from other species (e.g., Schindler et al., 2002). Sensitivity analyses have shown that accurate metabolic rate data are needed to construct realistic bioenergetics models (Kitchell et al., 1977; Bartell et al., 1986).

The allometric (size-dependent) influence on standard metabolic rate (SMR) in juvenile sandbar sharks was recently determined over the entire size range (42–92 cm PCL, 1–10 kg) characteristic of the Chesapeake Bay nursery area in flow-through respirometers for sharks treated with a neuromuscular blocker (Dowd et al., 2006). The best fitting allometric equation for SMR ($SMR = a \times M^b$) for 33 sharks at 24°C was

$$SMR_{24} = 120.0\ (\pm 17.3) M^{0.788\ (\pm 0.076)}, \quad (3)$$

where M = mass in kilograms; and
SMR = mgO_2 consumed per hour.

The values in parentheses are the standard errors of the allometric intercept and the allometric exponent estimates (hereafter $SMRa$ and $SMRb$, respectively).

Dowd et al. (2006) also determined the routine metabolic rate (the average oxygen consumption rate of a swimming shark) for 15 individual sandbar sharks at 24°C in an annular respirometer (diameter 1.67 m). The ratio of routine metabolic rate to SMR, corrected for the cost of swimming in a curved path in the respirometer (Weihs, 1981), averaged 1.62 ±0.11 (Dowd et al., 2006). This ratio was used in the model as a constant activity multiplier (ACT) to estimate field metabolic rate (*sensu* Winberg, 1960; Kitchell et al., 1977; Schindler et al., 2002). The ACT used is similar to those derived from field data for subadult *Negaprion brevirostris* (1.3; Sundström and Gruber, 1998) and juvenile *Sphyrna lewini* (1.45; Lowe, 2002). The sandbar shark ACT was assumed to remain constant for all age classes and over all temperatures (Dowd et al., 2006).

The effects of acute temperature changes (quantified as Q_{10}) on SMR for juvenile sandbar sharks (mass 1—10 kg) between 18° and 28°C have also been measured (Dowd et al., 2006). The overall mean Q_{10} (the relative increase in metabolic rate with temperature, scaled to a 10° temperature range) was 2.89 ±0.16 (n=43), was consistent over the size range of sharks tested, and was statistically indistinguishable among three treatments (18–24°C, 24–28°C, and 18–28°C). We assumed that the SMR Q_{10} remained constant throughout the simulation period.

For each day of the simulation, the Q_{10} was used to adjust the predicted SMR from Equation 3 to the simulated daily temperature (T) (equation adapted from Schmidt-Nielsen, 1997):

$$SMR_T = 10^{\left(\log SMR_{24} + \log Q_{10} \cdot \frac{(T-24)}{10}\right)}. \quad (4)$$

SMR_T was then multiplied by the ACT and by 24 hours to obtain the daily metabolic expenditure in mgO_2/day. Finally, this value was converted to daily metabolic energy utilization (RMR_D) by using the oxycalorific coefficient 13.59 J/mgO_2 (Elliott and Davison, 1975).

Specific dynamic action (SDA) Specific dynamic action represents the energetic cost of incorporation of digested amino acids into new proteins (Brown and Cameron, 1991). Although SDA varies with growth rate, or the protein content of ingested food (e.g., Ross et al., 1992), most bioenergetics models set SDA as a constant fraction of consumed energy (e.g., Hewett and Johnson, 1992). Fortunately, although SDA has been measured in only a few elasmobranch species, it is typically a relatively small fraction of consumed energy (DuPreez et al., 1988; Sims and Davies, 1994; Duffy, 1999; Ferry-Graham and Gibb, 2001). As an initial estimate, we assumed SDA to be 10% of consumed energy (Schindler et al., 2002).

Growth (*G*) Growth (*G*) is the change in energy stored in biomass and can be subdivided into somatic and reproductive growth outputs. We assumed the latter to be negligible because all the age classes in the sandbar shark bioenergetics model are at least 8 years from the age at maturity (Casey et al., 1985; Sminkey and Musick, 1995).

We employed a von Bertalanffy growth equation (Sminkey and Musick, 1995), based on a validated aging technique for sandbar sharks (Branstetter, 1987), to represent the precaudal length (PCL) of sharks of age *y* (*y*=0–5 **yr**) upon immigration (or birth) on May 15:

$$L_{yI} = L_{\infty}\left(1 - e^{-K(y-t_0)}\right) \quad (5)$$

where L_{∞} = 164 cm;
K = 0.089; and
t_0 = –3.8 years.

The PCL at emigration (L_{yE}) was determined by

$$L_{yE} = L_{yI} + p\,(L_{yI+1} - L_{yI}). \quad (6)$$

where p = the proportion of annual growth in PCL that occurs in the Chesapeake Bay nursery.

Analysis of vertebral rings indicates that annual growth of juvenile sandbar sharks occurs in two distinct phases: one period of rapid growth in the summer nurseries during which the sharks achieve roughly 75% of their annual growth in length, followed by a period of reduced somatic growth during the winter (Sminkey and Musick, 1995). Therefore, we assumed a p of 0.75 as an initial estimate. Limited tag-return data support this seasonal growth pattern. One juvenile (67 cm total length [TL] at tagging) was recaptured 0.5 km from the tagging location within the summer nursery in September 1998 by VIMS scientists; it had grown 3 cm TL after 44 days at liberty. Similarly, a juvenile sandbar shark of similar size that had been tagged and recaptured by NMFS scientists grew 3 cm in fork length (FL) (48–51 cm FL) over 62 days at liberty between mid-July and mid-September (Casey et al., 1985). In Delaware Bay, two sandbar sharks recaptured during the same summer grew 3 cm FL (45 cm flat tagging and 1 cm FL) (no size given) in 40 and 47 days at liberty, respectively (Merson and Pratt, 2001). In comparison, another juvenile (66 cm TL) was tagged in Chesapeake Bay in September 1995 and recaptured by VIMS scientists during the subsequent immigration period. This shark was at liberty for 225 days and grew only 3.5 cm TL during that time.

Both Medved et al. (1988) and Kohler et al. (1995) published equations relating mass to length for sandbar sharks. Because preliminary runs of the model demonstrated that these length-mass relationships yielded very similar results, we used the equation produced by Kohler et al. (1995) because it was derived from a larger number of individuals:

$$M = 0.0109\,FL^{3.0124}. \quad (7)$$

Fork length (FL) is in centimeters and mass (M) is in grams. Lengths were converted from PCL to FL and *vice versa* by using the regression (VIMS[1]):

$$FL = 1.0791\,PCL + 2.78. \quad (n=4385;\ r^2=0.99) \quad (8)$$

Specific growth rate (grams added per gram of body mass per day) was modeled by assuming that the mass of the shark increased by a constant proportion (x) in each of the n days of the simulation:

$$M_E - M_I = \sum_{D=1}^{n} x \times M_D. \quad (9)$$

M_D is the mass of the shark at the beginning of day D. No data exist to support an alternative pattern (e.g., growth varying with temperature or dissolved oxygen levels).

The mass of the shark on the first and last day (M_I and M_E, respectively) of the simulated nursery season was determined by using Equations 5–8. Fitted values for x in Equation 9 were on the order of 0.1–0.5% increases in mass per day. We used these values to calculate daily growth increments in grams per day and then multiplied by 5400 J/g of body mass (Cortes and Gruber, 1990; Lowe, 2002) to determine the daily increase in energy content.

Waste loss in feces (*F*) and excretions (*U*) A generally accepted value for total waste loss to excretions and fecal waste for carnivorous fishes and elasmobranchs is 27 ±3% of consumed energy (*C*) (Brett and Groves, 1979; e.g., Sundström and Gruber, 1998; Lowe, 2002; Schindler et al., 2002). This value was assumed for the sandbar shark in the present study, divided into F=0.20C and U=0.07C. Juvenile *N. brevirostris* have fecal waste losses between 38.1% and 16.9% (Wetherbee and Gruber, 1993), and excretory losses average 7% of ingested energy for a number of teleosts (Brett and Groves, 1979).

Water temperature data Surface and bottom water temperatures were obtained from the Chesapeake Bay Program's water quality database[2] for seven monitoring stations within the core sandbar shark nursery area in Chesapeake Bay for 1996–2002. Temperature measurements were averaged over all stations and over all years for each day of the simulation. The surface and bottom temperature readings were also averaged to obtain a mean water temperature for each day of the simulation in an average year. The simulated temperatures ranged from 16.8° to 27.9°C over the summer nursery season (mean 23.0° ±0.2°C).

Diet composition data Recent data detail the ontogenetic patterns of juvenile sandbar shark diet composition in and around Chesapeake Bay for sharks captured with longline and gillnet gears (Ellis, 2003). Diet data are represented by the index of relative importance. Index of relative importance combines the frequency, weight, and number of each prey type and is considered to have

Table 2

Diet composition data for juvenile sandbar sharks (*Carcharhinus plumbeus*) used to estimate daily rations and seasonal prey consumption. Prey species were grouped into four categories for each age class. Diet data, adapted from Ellis (2003), are expressed as index of relative importance. The average energetic content (J/g wet mass) of each prey type was calculated from data in Thayer et al. (1973).

Category	Representative species	Ages 0–1	Ages 2–3	Ages 4–5	Energy density (J/g)
Teleostei	Atlantic menhaden (*Brevoortia tyrannus*) Summer flounder (*Paralichthys dentatus*)	0.146	0.292	0.463	5050
Mollusca	Squids (*Loligo* spp.)	0.007	0.004	0.023	4390
Crustacea	Blue crab (*Callinectes sapidus*) Mantis shrimp (*Squilla empusa*)	0.847	0.672	0.421	4810
Elasmobranchii	primarily skates (*Raja* spp.)	—	0.031	0.094	5400

Table 3

Cohort sizes and estimated mean seasonal prey consumption in the lower Chesapeake Bay for each age class in the sandbar shark (*Carcharhinus plumbeus*) bioenergetics model. Cohort sizes are mean ±SE.

Age class	Initial cohort size[1]	Indexed cohort size[2]	Seasonal prey consumption (kg)[3]				
			Teleostei	Mollusca	Crustacea	Elasmobranchii	Total
0	2545 ±216	4377 ±1074	4236	207	24,667	—	29,110
1	2122 ±284	2626 ±645	3634	178	21,157	—	24,969
2	2083 ±398	1837±451	6684	100	15,385	716	22,885
3	1698 ±417	1698 ±417	7757	115	17,855	831	26,558
4	900 ±184	900 ±184	7754	380	7053	1575	16,762
5	188 ±40	188 ±40	1900	93	1728	386	4,107
Total	9537 ±313	11,627 ±2483	31,965	1073	87,844	3,508	124,391

[1] Estimates are from Sminkey (1994).
[2] We retained the initial cohort size estimates for ages 3–5.
[3] Estimated by using mean indexed cohort size.

less bias than other diet indices (Cortes, 1997). For the present study, prey species were grouped into four categories for each age class of shark: teleost fishes, mollusks, crustaceans, and elasmobranchs (Table 2). The proportion of each prey type in the diet and the mean energy content values for each category (calculated from data in Thayer et al., 1973) were used to convert daily energy ration (kJ/d) to daily ration (percent body mass per day, %BM/d). Diet composition was assumed to remain constant during the simulation period. The average daily ration and total seasonal prey consumption were calculated for individuals of each age class.

Population estimates The relative abundance and size-class composition of the seasonal nursery population were estimated from catch per unit of effort (CPUE) data (Musick et al., 1993; VIMS[1]). Sminkey (1994) used virtual population analysis to estimate the sandbar shark cohort sizes in the Chesapeake Bay nursery from the VIMS Shark Longline Survey data, using the standard Mustad™ 9/0 J hooks between 1989 and 1993 (Table 3). However, the standard hooks select for larger animals, yielding underestimates of abundance for ages 0–2 years. Therefore, we indexed the VIMS CPUE data for ages 0–2, using smaller Mustad™ 12/0 circle hooks against the CPUE for larger hooks for 25 longline sets between 1997 and 2002 when both gears were fished simultaneously at the two lower Chesapeake Bay survey stations. We then used this index to produce a more realistic population age structure (Table 3). The mean adjusted nursery population size was 11,627 ±2483 individuals.

For simplicity, we assumed negligible mortality and zero emigration of juvenile sharks during the simulation period. Consequently, the revised cohort sizes were held constant throughout the simulation period. Low natural mortality rates would be expected for these sharks, particularly in light of the near absence of large coastal shark predators in the nursery (Musick et al., 1993). Tracking, tagging, and survey data all indicate that juvenile sandbar sharks remain within the nursery throughout the summer (Grubbs et al., in press; Merson and Pratt, 2001).

Model calculations

For each daily time step of the model and for each age class, RMR_D and G_D were calculated as described above. These estimates were used to solve for daily consumption in joules in Equation 2, where *SDA*, *U*, and *F* are the fractions of consumption described above. These daily energy consumption estimates were summed to determine total energy consumption for an average individual of each age class during the entire stay in the Chesapeake Bay nursery. Mean daily energy ration (DER) was calculated in kJ/d. The daily energy ration was also expressed as a percentage of the average total energy content (%DER) for each day:

$$\%DER = 100 \cdot \frac{C_D}{\left(\frac{M_D + M_{D+1}}{2} \cdot 5400\right)}. \quad (10)$$

Finally, gross conversion efficiency (K_1), the fraction of consumed energy that is devoted to growth, was calculated for each day:

$$K_{1_D} = \frac{G_D}{C_D}. \quad (11)$$

This value was used as a general test of the model outputs.

Error analysis

Static models were run by using the initial parameter estimates described above to determine point estimates of consumption. *SDA* and energy losses in *U* and *F* were modeled as constant fractions of consumption. The initial choices of these values, therefore, had a direct effect on the predicted consumption rates. Further, a number of the model parameters were measured with some uncertainty. A stochastic, Monte Carlo simulation routine (Crystal Ball© 2000 Academic Edition, vers. 5.2.2, Decisioneering, Inc., Denver, CO) was used to assess this uncertainty with error analysis (Bartell et al., 1986). Error analysis is particularly useful for evaluating model sensitivity to parameters that enter the model in a nonlinear fashion (Bartell et al., 1986), such as the SMR allometric exponent (SMRb) and allometric constant (SMRa) and the Q_{10}. The simulation randomly drew values from probability distributions for each model parameter (Table 1) for each of the 2000 Monte Carlo iterations. The model parameters were ranked in importance by their relative contribution to the variance of the stochastic model outputs (Bartell et al., 1986).

Results

Consumption rates

The model predicted mean daily energy rations (DER) increasing from 233 ±5 kJ/d (%DER=1.95 ±0.03%) for young-of-the-year to 784 ±16 kJ/d (%DER=1.20 ±0.02%) for an age-5 juvenile. These values correspond to prey consumption rates of 2.17 ±0.03%BM/d and 1.30 ±0.02%BM/d, respectively (Table 4). The predicted daily rations for a given age class over the course of the simulation period fluctuated with temperature because of the thermal influence on metabolic rate.

Table 4

Gross conversion efficiency (K_1), daily energy ration (DER), daily ration (DR), and total seasonal prey consumption (C_{tot}) for individuals of each age-class of the sandbar shark (*Carcharhinus plumbeus*) in the bioenergetics model. DER and DR were averaged over the 138 days of the simulation (mean ±SE).

Age class	K_1	DER (kJ/d)	DR (%BM/d)	C_{tot} (kg)
0	0.16	233 ±5	2.17 ±0.03	6.6
1	0.15	333 ±7	1.89 ±0.03	9.5
2	0.13	442 ±9	1.67 ±0.03	12.5
3	0.12	555 ±11	1.52 ±0.03	15.6
4	0.11	669 ±14	1.39 ±0.02	18.6
5	0.10	784 ±16	1.30 ±0.02	21.8

During the 4.5-month stay in the Chesapeake Bay nursery area, the static model predicted total energy consumption of 269% of the total energy content for an age-0 shark (~32,000 kJ), declining to 165% (~108,000 kJ) for age-5 sharks. When merged with diet composition data, the model predicted that an age-0 shark would consume 6.6 kg (300% average BM) of prey per summer, and an age-5 juvenile would consume 21.8 kg (180% average BM). Therefore, the total sandbar shark population would consume 124,400 kg of prey over the course of the summer in the Chesapeake Bay nursery area (Table 3).

The average K_1 declined quickly with age from 16.3 ±0.3% of consumed energy for age-0 sharks to 10.0 ±0.2% of consumed energy by age five. Because growth plus routine metabolism comprised a constant proportion of the total energy budget in the static model, the proportion of consumption devoted to metabolism increased with age. Metabolism for age-0 sandbar sharks accounted for roughly 46% of ingested energy, increasing to 53% of the energy budget for age-5 juveniles. When growth was set to zero, we calculated the maintenance rations to be 63–80% of the rations when growth was included.

Error analysis

The relative contributions of each of the input parameters to the variance of the model outputs exhibited similar patterns for all age classes (Fig. 1). The von Bertalanffy parameters predicting size at age (L_∞, K) had consistently high ranks for their contribution to model variance, as did those describing the allometric scaling of standard metabolic rate (*SMRa*, *SMRb*). *F* also contributed significantly to the variance of the model outputs for all age classes (Fig. 1). The contributions

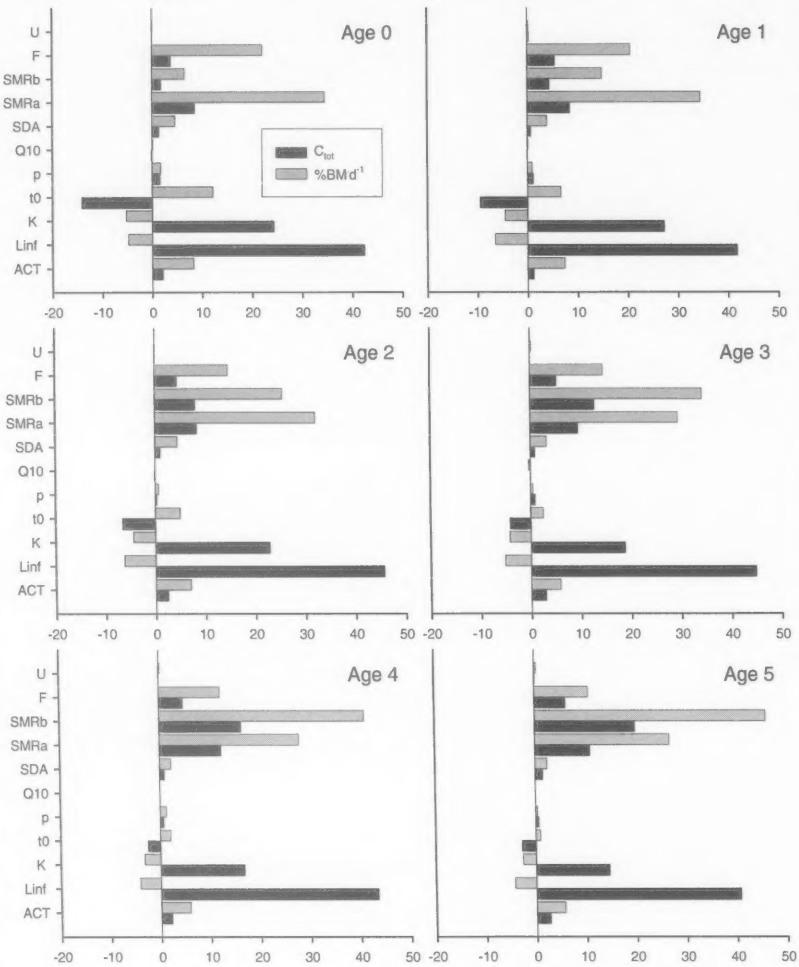

Figure 1

Results of the error analyses for the sandbar shark (*Carcharhinus plumbeus*) bioenergetics model for ages 0–5 years, using the eleven parameters and distributions from Table 1 in 2000 Monte Carlo simulations. The horizontal axis is the percentage contribution of the variable of interest to the variance in two model predictions: total seasonal prey consumption in kg (C_{tot}, black bars) and mean daily ration (%BM/d, grey bars). Positive values indicate that an increase in the parameter yields an increase in the model output, and negative values indicate the opposite. See text for definitions of parameter abbreviations along the *y* axix.

of uncertainty in U, p, and Q_{10} were negligible for all age classes.

The Monte Carlo simulations predicted mean seasonal energy consumption rates 11–15% higher than those derived by using the static model. This elevation was primarily due to the fact that SDA and fecal waste (F) were allowed to comprise larger proportions of consumption than in the static model runs.

Discussion

Comparison with previous results

The mean daily rations for age-0 juvenile sandbar sharks predicted from our bioenergetics model (2.17 %BM/d, average M=2.2 kg) were higher than those previously reported (1.32 %BM/d, M=1.9 kg, Medved et al., 1988;

1.49%BM/d, M=1.7 kg, Stillwell and Kohler, 1993). This difference was partly due to the incorporation of species-specific routine metabolic rate data into our model, which were 8–15% higher than values from the spiny dogfish (*Squalus acanthias*) used in earlier models. Earlier models also estimated daily ration at a mean temperature over the entire year, whereas our model incorporated seasonal temperature shifts and the resulting effects on metabolic rate using the Q_{10}. Test runs of our model were used to predict daily rations over the winter, assuming that the diet composition was the same, 25% of annual growth occurred in the winter (Sminkey and Musick, 1995), and average water temperature was 14°C (Springer, 1960). These model runs predicted daily rations less than half (<1%BM/d) of those estimated for the summer nursery season. More data, however, are needed on the biology of sandbar sharks in the winter nursery grounds in order to develop an accurate year-round bioenergetics model.

Sandbar shark daily consumption rates have also been estimated by using meal size and frequency, as well as gastric evacuation rates. Our model's predicted consumption rates (1.30–2.17 %BM/d) support estimates based on meal size and frequency. The reconstructed meal size for juvenile sandbar sharks in Chincoteague Bay, based on stage of digestion estimates, was 4.23 ±0.31% BM (Medved et al., 1988). Given the sandbar shark's 70–92 hour gastric evacuation rate (Medved, 1985), as well as the high proportion of sharks landed with empty stomachs (17.9–20.0%) (Medved and Marshall, 1981; Medved et al., 1985; Stillwell and Kohler, 1993; Ellis, 2003), it seems likely that 48–72 hours pass between significant feeding events (Medved et al., 1985). Therefore, the reconstructed meal sizes correspond to daily consumption rates of 2.12–1.41% BM/d. In contrast, gastric evacuation models predicted juvenile sandbar shark daily rations (0.93% BM/d to 1.07% BMd; Medved et al., 1988) lower than our bioenergetics model. However, the data probably violated the gastric evacuation models' assumptions of continuous feeding and that time between meals exceeds digestion time (reviewed by Cortes, 1997).

The estimated sandbar shark daily rations are comparable to those for other active shark species. For example, the estimated daily rations for a 1-kg *N. brevirostris* and a 0.76-kg *S. lewini* were 2.62% BM/d and 2.9–3.9% BM/d, respectively (Gruber, 1985; Lowe, 2002). The sandbar shark daily rations were averaged over the entire simulated nursery season, during which temperature fluctuated by 10°C. Predicted daily rations in mid-summer were frequently higher than 3.0% BM/d.

The predicted mean gross conversion efficiency from our model (0.10–0.16) was similar to estimates for bull sharks (*Carcharhinus leucas*) fed to satiation in captivity (0.05–0.12, Schmid and Murru, 1994) and for juvenile lemon sharks (*N. brevirostris*) in the wild (0.10–0.13, Cortes and Gruber, 1994).

Parameter uncertainty

The largest potential sources of error in the model were L_∞, K, *SMRa*, and *SMRb* (Fig. 1). Fortunately, the von Bertalanffy growth parameters (L_∞, K) and the SMR allometric scaling parameters (*SMRa* and *SMRb*) are among the best known for juvenile sandbar sharks, and the initial estimates used are considered reliable. Metabolic rate may also be impacted by osmoregulatory costs incurred by penetrating the less saline regions (~20–25 ppt) of the Chesapeake Bay nursery area (Chan and Wong, 1977; Meloni et al., 2002). Future studies should investigate this possibility. Other confounding factors which will alter metabolic rate estimates associated with routine swimming behavior include movement of the animals with dominant tidal currents or burst swimming followed by oxygen debt repayments (or both factors) (e.g., Kerr, 1982; Boisclair and Leggett, 1989). Although these factors may affect ACT estimates, field tracking data from juvenile sandbar sharks indicate that mean rates of movement (converted to body lengths per second, BL/s) in the wild (0.23 BL/s, Huish and Benedict[3]; 0.46 BL/s, Medved and Marshall, 1983; 0.59 BL/s, Grubbs, 2001) are comparable with laboratory swimming speeds used to estimate the ACT (mean 0.55 BL/s; Dowd et al, 2006).

The effects of temperature on metabolism were not important in the error analyses, but two points merit consideration. Seasonal (e.g., winter vs. summer) metabolic rate Q_{10} may be lower than Q_{10} in response to acute temperature changes (Carlson and Parsons, 1999); future studies should address this possibility in sandbar sharks. The averaging of surface and bottom water temperatures in the model potentially obfuscated short-term changes in metabolic rate caused by sharks crossing the thermocline. Energetic implications of such short-term movements could be investigated with more detailed spatial models, but such an approach lies outside the scope of the present study.

Uncertainty in the fecal waste parameter accounted for a large portion of the variance in the stochastic model outputs, indicating that F should be investigated in sandbar sharks to refine the bioenergetics model. The effects of the slow gastric evacuation rate of the sandbar shark on the magnitude of the waste and SDA parameters are unknown.

One of the implicit assumptions of our model is that all energy spent is derived from food. Because juvenile sandbar sharks in the Chesapeake Bay nursery appear to grow steadily and rapidly (Sminkey and Musick, 1995), the assumption that the vast majority of energy is derived from food and not from energy reserves is probably justified. However, little is known about the feeding habits of sandbar sharks during their seasonal migrations or during their time in the winter nursery. At these times stored energy may play a greater role in the energy budget. Seasonal changes in energy content occur in Atlantic sharpnose sharks (*Rhizoprionodon*

[3] Huish and Benedict (1977) published their results under the species name for the dusky shark (*Carcharhinus obscurus*), but Grubbs (2001) noted that the size of the animals tracked was smaller than the size at birth for *C. obscurus*. Misidentification of the congeneric sandbar and dusky sharks is common.

terraenovae) (Hoffmayer, 2003); if such changes occur in sandbar sharks, these fluctuations could also affect the model's consumption estimates.

Ecosystem interactions

Our results downplay the top-down role of sandbar sharks in the trophic economy of the lower Chesapeake Bay. The model results presented above predict that juvenile sandbar sharks consume ~120,000 kg of prey in an average summer in the nursery. In comparison, the estimated annual prey consumption rates of the dominant teleost piscivores (bluefish, *P. saltatrix*; striped bass, *M. saxatilis*; and weakfish, *Cynoscion regalis*) in Chesapeake Bay were 27,000,000 kg, 10,000,000 kg, and 5,000,000 kg, respectively (Hartman and Brandt, 1995a). Moreover, the seasonal consumption of prey species by juvenile sandbar sharks is insignificant compared to fisheries landings. The total predicted consumption of Crustacea and Teleostei by juvenile sandbar sharks equals only 0.57% and 0.01% of the annual commercial landings of blue crabs (*C. sapidus*) and Atlantic menhaden (*B. tyrannus*) in Virginia, respectively (U.S. Department of Commerce[4]).

Bottom-up effects on sharks as apex predators are possible if lower trophic levels are overfished, but the apparent opportunistic foraging strategy of sandbar sharks (Medved and Marshall, 1981; Medved et al., 1985; Stillwell and Kohler, 1993; Ellis, 2003) probably reduces their vulnerability to declines of specific prey species (Stevens et al., 2000). However, if current fishery landings in Chesapeake Bay are not sustainable, the dietary overlap between the dominant piscivorous teleost species (Hartman and Brandt, 1995b) and sandbar sharks could lead to competition among these predators for limited prey.

Conclusions

An updated sandbar shark bioenergetics model predicts higher consumption rates than earlier bioenergetics estimates, but the daily ration estimates generally agree with reconstructed meal sizes from stomach contents data. Our results will be useful for ongoing efforts to build ecosystem-wide trophic models for the lower Chesapeake Bay.

As the sandbar shark population slowly recovers from overfishing, the contributions of the summer nursery grounds of the lower Chesapeake Bay to juvenile growth and survival will remain critical. Meanwhile, the slow growth rate and low consumption rate of these long-lived elasmobranchs in a complex trophic system may indicate a limited top-down ecosystem role for sandbar sharks in Chesapeake Bay. Our results support the conclusion that the effects of anthropogenic activities—fisheries and other activities—on shark populations often greatly outweigh the effects of these populations on their ecosystems (Stevens et al., 2000; Bush and Holland, 2002; Kitchell et al., 2002; Baum et al., 2003; Bascompte et al., 2005).

[4] United States Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service. Commercial Fishery Landings Database. Website: http://www.st.nmfs.gov/st1/commercial/index.html [accessed May 2004.]

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Depredation of catch by bottlenose dolphins (*Tursiops truncatus*) in the Florida king mackerel (*Scomberomorus cavalla*) troll fishery

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Abstract—We documented depredation by bottlenose dolphins (*Tursiops truncatus*) in the Florida king mackerel (*Scomberomorus cavalla*) troll fishery. Between March and June 2003, we conducted 26 interviews of charter and commercial fishermen in Islamorada, Florida, and 23 along Florida's east coast from Fort Pierce south to Lake Worth Inlet. All fishermen indicated they had observed bottlenose dolphins depredating bait or catch—king mackerel being the species most often taken by dolphins. During on-board observations of depredation between March and June 2003, we found that dolphins took 6% of king mackerel caught by charter fishermen and 20% of fish caught by commercial fishermen. We concluded that depredation by bottlenose dolphin occurs commonly in this fishery and has the potential to incur a significant economic cost to king mackerel fishermen. To address this concern, we conducted preliminary tests of a gear modification designed to reduce depredation in the king mackerel fishery between December 2003 and January 2004. These tests demonstrated that a modification to the outrigger planer will successfully deter bottlenose dolphins from engaging in depredation, without causing a reduction in catch.

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Depredation is the removal of or damage to captured fish or bait caused by marine predators. Evidence of depredation exists for several pinniped and cetacean species (Yano and Dahlheim, 1995; Reeves et al.[1]; NRC, 2003). A recent increase in the number of reports of depredation by marine mammals may reflect changes in fishing effort, increased spatial overlap between these predators and fisheries, or behavioral learning among marine mammals (Donoghue et al.[2]). With a rapidly growing human population, fishing effort in coastal regions will likely continue to increase, causing even greater conflicts between fisheries and marine mammal populations throughout the world's oceans (Read, 2005).

Marine mammals engaging in depredation cause damage to fishing gear, decrease the value and quantity of catches, and reduce catch by dispersing fish (Reeves et al.[1]). Depredation may benefit marine mammals by increasing foraging success, but the behavior, habitat, and distribution of mammals may change as they frequent areas of high fishing effort (Reeves et al.[1]). Harmful consequences of depredation to marine mammals may include injury or mortality from entanglement with fishing gear or from the retaliatory measures of angry fishermen.

Our purpose in this study was to document the extent, nature, and cost of depredation by bottlenose dolphins (*Tursiops truncatus*) in the king mackerel (*Scomberomorus cavalla*) charter and commercial fisheries of Florida. There have been previous anecdotal reports of depredation by dolphins in this fishery (Odell, 1975), but no systematic study of these interactions has been conducted. We also worked with fishermen to identify potential tools that would deter dolphins from engaging in depredation. Other studies have employed this approach with considerable success. For example, Noke and Odell (2002) modified the design of crab pots, and thus prevented dolphins

[1] Reeves, R. R., A. J. Read, and G. Notarbartolo di Sciara (eds.). 2001. Report of the workshop on interactions between dolphins and fisheries in the Mediterranean: evaluation of mitigation alternatives, 44 p. Istituto Centrale per la Ricerca Applicata al Mare, Rome, Italy. Website: http://www.cetaceanbycatch.org/Papers/Reeves.pdf [acessed on 12 March 2004].

[2] Donoghue, M., R. R. Reeves, and G. Stone. 2003. Report on the workshop on interactions between cetaceans and longline fisheries held in Apia, Samoa, November 2002. New England Aquarium Aquatic Forum Series Report 03-1, 44 p. Website: http://neaq2.securesites.net/scilearn/conservation/LonglineReport2002.pdf [accessed on 17 January 2004].

from opening pot doors and taking bait fish. Melvin et al. (1999) demonstrated a reduction in seabird depredation of salmon gill nets by combining the use of acoustic devices and mesh panels strategically placed in the upper portion of the gillnet as a deterrent to seabirds.

King mackerel are distributed along the east coast of the United States from Massachusetts to the Gulf of Mexico and Caribbean Sea (Gold et al., 2002). Two stocks of king mackerel occur in Florida, one that migrates along the Atlantic coast and the other that is found in the Gulf of Mexico (Schaefer and Fable, 1994; Gold et al., 2002).

King mackerel are captured primarily by trolling, in which a fishing vessel trails several fishing lines—either from fishing poles (on charter vessels) or from reels (on commercial boats). Both charter and commercial vessels use outriggers that help to prevent entanglement of multiple lines. Trolling is generally considered to be a "clean" fishery with little bycatch. By varying the size of hooks, lures, and choice of bait, fishermen effectively target particular species and limit the bycatch of undesired species (Alverson et al., 1994). Nontarget species are generally released and have a high probability of survival.

Commercial fishing operations in the United States yielded over 4.8 million pounds of king and cero mackerel (*Scomberomorus regalis*) during 2001. This commercial fishery was valued at almost seven million dollars, more than half of which was landed in Florida (O'Bannon, 2002). During 2001–02, commercial fishermen captured more than two million tons of Atlantic king mackerel, sixty percent of which was caught in Florida, whereas recreational fishermen reported catching about four million tons of fish from the same stock, and about fifty-eight percent of this catch was taken in Florida (NMFS[3]).

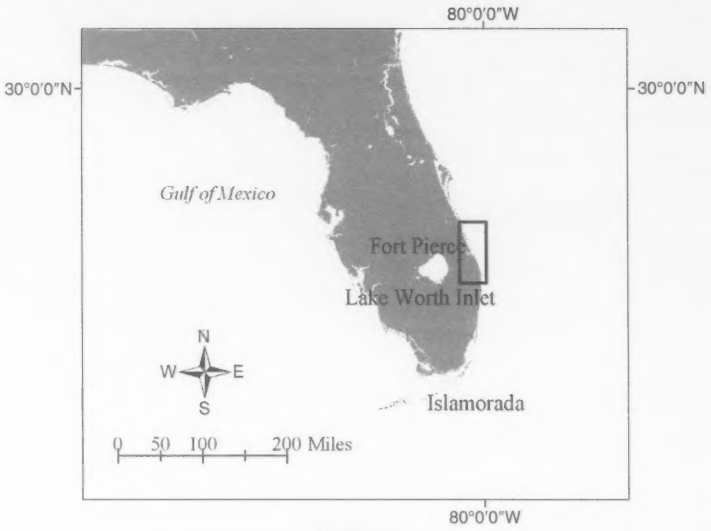

Figure 1

Survey area for bottlenose dolphin (*Tursiops truncatus*) depredation on the king mackerel (*Scomberomorus cavalla*) fishery in Florida. (Source of map: Florida Fish and Wildlife Conservation Commission; adapted by present authors.)

Materials and methods

Study sites

We selected two coastal regions of Florida: 1) Islamorada in the Florida Keys and 2) along the eastern coast, from Fort Pierce south to Lake Worth Inlet, for our study (Fig. 1). These regions represent areas in which commercial and charter fisheries for king mackerel exist during at least part of the year. Islamorada draws thousands of tourists each year to its charter fleet; the east coast of Florida boasts a thriving commercial king mackerel fishery.

Interviews with fishermen

From March through June 2003, we interviewed fishermen, using the face-to-face method of Rea and Parker (1997). We selected captains of offshore fishing charter boats or commercial king mackerel fishermen in the study sites to participate in this study. Because of the multi-use nature of fishing vessels, we included commercial, charter, and recreational vessels as options of vessel type on the survey.

Observations of dolphins

We conducted observations from the flying bridge of the charter boats and from the stern of the commercial vessels from March to June 2003. We recorded positional coordinates every 30 minutes with a hand-held GPS unit. During each 30-minute interval, we recorded vessel activity (transit to and from fishing grounds, or active fishing) and further categorized the fishing activity, depending on the target species.

For each 30-minute period, we recorded the behavior and estimated the number of dolphins sighted during the interval. We defined the following behavioral categories:

Depredation	a dolphin was observed consuming bait or captured fish from the lines
Begging	a dolphin approached a vessel in order to obtain food

[3] NMFS (National Marine Fisheries Service). 2003. Stock assessment analyses on spanish and king mackerel stocks, 147 p. Prepared for the 2003 mackerel stock assessment panel meeting. Sustainable Fisheries Division Contribution SFD/2003-0008, NMFS, Southeast Fisheries Science Center, Sustainable Fisheries Division, 75 Virginia Beach Drive, Miami, FL 33149.

Eating discarded bait	a dolphin consumed bait thrown from a fishing vessel
Milling near the boat but not interacting with the boat	a dolphin was in the same area as the fishing vessel but did not seek food or become entangled in gear.
Following the boat	a dolphin was actively following or pursuing the boat
Passing the boat or being passed by the boat	a dolphin was observed traveling or was passed by the vessel, but the dolphin neither followed nor interacted with the vessel

Impact on the king mackerel fishery

To assess the extent and impact of depredation on the king mackerel fishery, we recorded the type of fishing gear, the number and species of fish caught, and the number and species of fish lost or damaged by depredation during each 30-minute fishing interval. We attributed lost fish to bottlenose dolphin depredation if we observed dolphins following the boat or chasing the fish. We recorded the species of the fish if a definitive part of the fish was retrieved or if we observed the fish before depredation occurred. We also recorded the fishermen's response to depredation. The categories of response included leaving fishing grounds, ignoring dolphin depredation, throwing objects or shooting, cutting fishing line, or increasing boat speed.

Testing a deterrence device

We also worked with fishermen to devise and test a deterrence device to be used on outriggers of commercial fishing vessels. The device was equipped with a planer that is used on outrigger lines. An outrigger release clip was secured to the back of the planer (Fig. 2). The bait line passed through the outrigger clip, which released when a fish bit on the bait. The clip also released a metal wire that was attached to the bait line. The wire traveled towards the fish and flapped around the fish at the end of the bait line, making it difficult for a dolphin to approach the fish.

We tested the device on commercial fishing vessels in Fort Pierce during December 2003 and January 2004. We randomly placed the device on one of two outriggers, noting on which of the two outriggers the device was placed and the time and GPS coordinates for each event. An event occurred when the fishing line was placed in or taken out of the water and when a fish was caught or depredated. We recorded the number and species of each fish that was caught, taken, or damaged.

Results

Interviews with fishermen

We conducted interviews with 26 king mackerel boat operators in Islamorada and 23 operators along Florida's east coast. Several individuals indicated that their boats served multiple purposes or that they operated different types of boats during different times of the year (Table 1).

All fishermen responded that they saw or interacted with bottlenose dolphins while fishing. Forty-seven fishermen provided useful responses to questions regarding depredation; all of these respondents indicated they had observed dolphins taking bait or catch. Other reported interactions included entanglement in fishing gear (10.6%), begging (4%), and eating discarded bait (10.6%). Ninety-seven percent of participating fishermen reported that king mackerel were taken by bottlenose dolphins. King mackerel was the species most often identified as being taken by bottlenose dolphins, but other fish reportedly taken included amberjack (*Seriola*

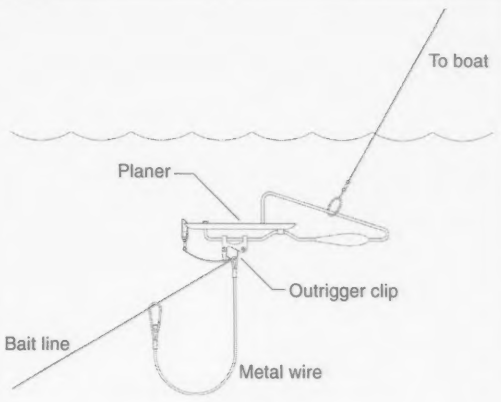

Figure 2

A device designed to reduce bottlenose dolphin (*Tursiops truncatus*) depredation in the commercial king mackerel (*Scomberomorus cavalla*) troll fishery. The device is created with an outrigger clip secured to the back of a planer. The wire, attached at one end to the outrigger clip and clipped at the other end to the bait line, is released from the outrigger clip when a fish bites the line, and it travels to the end of the bait line. At the end of the bait line, the metal wire flaps about and deters a dolphin from taking a captured fish. (Diagram by Eric Blankfield).

Table 1

Vessel type and location of respondents in interview surveys of fishermen for a study of bottlenose dolphin depredation in the Florida king mackerel fishery. Nine individuals selected more than one vessel type.

	Commercial	Charter	Recreational
Islamorada	1	23	3
East Coast	17	12	2

fasciata), blackfin tuna (*Thunnus atlanticus*), and Spanish mackerel (*Scomberomorus maculatus*) (Fig. 3).

More than half of the fishermen we interviewed indicated that the interactions with bottlenose dolphins occurred either daily or several times a week. In Islamorada, fishermen indicated that winter was the season with the highest number of interactions, and along the east coast of Florida, most interactions occurred during spring (Fig. 4). Most interviewees (76.6%) indicated they believed that bottlenose dolphin conflicts with fishing efforts had increased over the past several years. The vast majority (94%) of commercial fishermen indicated that bottlenose dolphin depredation was causing a significant economic loss, although a smaller number of charter fishermen held this view (Fig. 5). A Mann Whitney test indicated a significantly higher perceived economic loss from depredation for commercial fishermen than for charter fishermen ($P<0.001$).

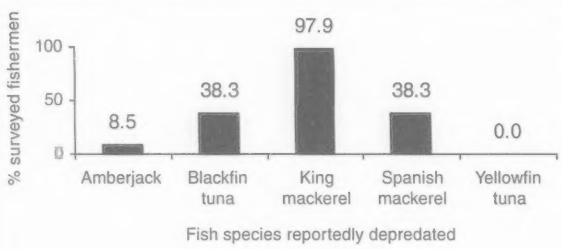

Figure 3

Percent of surveyed fishermen identifying fish species that are depredated by bottlenose dolphins (*Tursiops truncatus*) in the Florida king mackerel (*Scomberomorus cavalla*) fishery. No individuals reported depredation of yellowfin tuna (*Thunnus albacares*), and all of the fishermen reported depredation of at least one of the listed fish species.

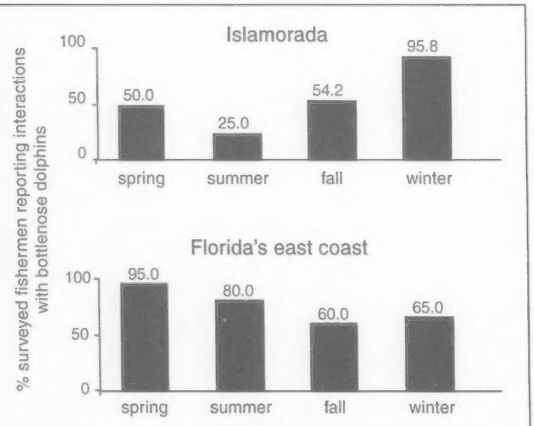

Figure 4

Percent of surveyed fishermen reporting interactions with bottlenose dolphins (*Tursiops truncatus*) during each season in the king mackerel (*Scomberomorus cavalla*) troll fishery along Florida's east coast and off Islamorada, Florida.

Observations of dolphins

We made observations from five charter boats in Islamorada and from four charter and four commercial boats along the east coast. We spent 41 hours conducting field observations in Islamorada and 85 hours along the east coast. We observed dolphins taking or attempting to take catch, following the boat, feeding or milling near boat with no interactions, and passing by the boat (Fig. 6). All the observations of bottlenose dolphins following the vessel occurred when the vessel was fishing for king mackerel.

We observed 15 fish taken or damaged by bottlenose dolphins. Depredation by bottlenose dolphins was characterized by an abnormal jerk on the line after a fish was known to have taken the bait. For charter fishermen, 6% of the king mackerel catches were taken or damaged by bottlenose dolphins. Depredation events occurred more frequently on commercial fishing vessels, where bottlenose dolphins took almost 20% of the king mackerel. We observed thirteen depredation events on commercial vessels and single depredation events while aboard charter vessels on Florida's east coast and off Islamorada. All depredation events occurred during fishing operations for king mackerel. Only one event occurred in Florida's state waters (within three nautical miles from shore); all others occurred between three and twelve nautical miles offshore. In both study areas, the number of dolphins observed while depredation occurred ranged from one to three dolphins, although other dolphins were often in the same area, following or engaging in depredation with nearby fishing vessels.

It proved impossible to photograph bottlenose dolphin dorsal fins during acts of depredation, because of the nature of the interaction. Bottlenose dolphins typically remained too far from the vessel to allow useful photographs to be obtained. When a fish was caught, the dolphins would swim rapidly towards the boat with their dorsal fins directly below the surface in order to take the fish. After taking the fish, the dolphins would surface well away from the boat.

Impact on the king mackerel fishery

During the fifteen depredation events, we observed lost and damaged fish and loss of gear, including line, lures, hooks, and occasionally planers. Fishermen typically responded to depredation by leaving the area or by ignoring the bottlenose dolphins. In one instance, we observed a charter boat captain shooting a gun into the water to protect his catch and fishing gear. We also observed the use of bird bangers, sound-creating devices similar to a

gun shooting blanks, in response to depredation. Anecdotal accounts of the use of seal bombs, guns, and bird bangers were also reported by commercial and charter fishermen.

Experimental testing of deterrence device

In three cases when the device was in use, bottlenose dolphins approached a king mackerel on the fishing line, but left the fish apparently after they detected the device. The number of fish caught per hour for each outrigger was 1.48. A *t*-test demonstrated no significant difference exists between the rate of fish caught by each outrigger when the device was not used (P=0.99). We also found no difference in the number of fish caught per hour by outriggers equipped with the device (1.40) with those without the device. The device did not cause a reduction in catch of targeted species (P=0.83).

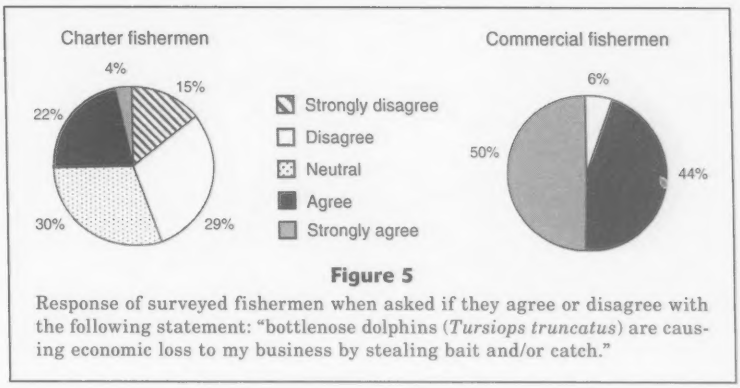

Figure 5

Response of surveyed fishermen when asked if they agree or disagree with the following statement: "bottlenose dolphins (*Tursiops truncatus*) are causing economic loss to my business by stealing bait and/or catch."

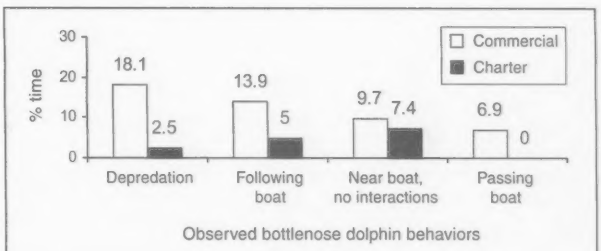

Figure 6

Bottlenose dolphin (*Tursiops truncatus*) behaviors observed from king mackerel (*Scomberomorus cavalla*) fishing vessels.

Discussion

We documented frequent depredation in both the king mackerel charter and commercial troll fisheries in southeastern Florida. All commercial and charter fishermen indicated that they experienced bottlenose dolphins taking their bait or catch. During our observations, approximately one in every five fish caught by commercial fishermen was lost to bottlenose dolphins, but only 6% of catch was lost by charter fishermen. This difference in depredation rates may be attributed to seasonal variation in the distribution of king mackerel or differences in the gear used by the two fishery sectors. Fishermen in Islamorada reported that most conflicts with dolphins occur in the winter. Because of the highly migratory nature of king mackerel and the mixing of the South Atlantic and Gulf stocks in the winter in the Florida Keys, we anticipated that a higher depredation rate would be experienced by the charter fishery in winter (Gold et al., 2002). We observed commercial fishing operations along Florida's east coast during the season with the most reported conflicts. Depredation rates along the east coast, however, may be even higher in the spring than at the end of spring and summer when our observations were made.

In addition, commercial fishermen target king mackerel, whereas charter boats use fishing gear that targets a variety of fish species, including amberjack, barracuda (*Sphyraena obtusata*), and bonito (*Sarda sarda*). The higher depredation rates encountered by commercial fishermen may result from the regular capture of king mackerel compared to the various species caught by charter boats during a fishing trip. In addition to king mackerel, species that were reported taken by both commercial and charter boat fishermen included Spanish mackerel, amberjack, and blackfin tuna. We did not observe depredation of these species, most likely because they were rarely caught during our study. However, depredation of these species has been reported from Spanish mackerel fisheries elsewhere (Read et al., 2003).

We observed bottlenose dolphins engaging in depredation only while the vessels were fishing for king mackerel. Bottlenose dolphins do not generally prey on king mackerel; Barros (1993) did not find king mackerel in the stomach contents of any stranded dolphins in Florida. Exploitation of fisheries by marine mammals may introduce a new food resource that was either not previously available or used, as seen in the case of pilot whales (*Globicephala spp.*) that feed on Atlantic mackerel (*Scomber scombrus*) in trawl fisheries off the northeastern United States (Waring et al., 1990; Gannon et al., 1997) and in the case of killer whales (*Orcinus orca*) that prey on swordfish (*Xiphias gladius*) hooked on longlines in southern Brazil (Secchi and Vaske, 1998). It is likely that fishing affects not only the diet but also the behavior and spatial distribution of bottlenose dolphins (Leatherwood, 1975; Chilvers et al., 2003). The bottlenose dolphins in this study may spend less time foraging, but as indicated by the observed depredation

of king mackerel, the diet and possibly the distribution of these animals is impacted by their interaction with the fishery.

In this study, fishermen reported observing female bottlenose dolphins "teaching" their calves how to engage in depredation, indicating a behavioral transmission of knowledge. Depredation of king mackerel by bottlenose dolphins may have resulted from a learned behavior that results in a low-cost foraging specialization.

Over three quarters of interviewed fishermen reported increasing conflicts with bottlenose dolphins. The frequency of these interactions most likely result from a combination of factors, including behavioral learning, increasing fishing effort, and spatial overlap and resource competition between cetaceans and fisheries (Donoghue et al.[2]). In addition, an upsurge in depredation may be correlated with a rise in troll fishing effort that resulted from the July 1995 statewide ban of gill nets in Florida (Wells et al., 1998). The increase in depredation places bottlenose dolphins in close proximity to fishing vessels and gear, increasing the risk of injury or death to the dolphins. It is unknown if the dolphins in this study were injured by hooks. Although we did not observe entanglement in this study, entanglement in and ingestion of fishing gear by bottlenose dolphins could result from depredation. Hucke-Gaete et al. (2004) observed a fatal entanglement of a sperm whale (*Physeter macrocephalus*), likely engaging in depredation, in a longline fishery off southern Chile. Monofilament fishing line does not degrade rapidly, and injury or death can result from the entanglement in or ingestion of fishing gear (Mann et al., 1995). Previous research has documented the deaths of bottlenose dolphins from entanglement (Wells et al., 1998) and from ingestion of monofilament line (Gorzelany, 1998).

As a result of lost or damaged gear and catch, fishermen experience economic loss from these interactions. Commercial fishermen reported significantly higher economic losses than charter boat fishermen. Our observations confirm the potential for high economic loss by commercial fishermen due to lost fishing gear and depredation. Because of the cost to commercial fishermen and risk to marine mammal safety, we investigated gear modification as a potential solution to reduce these conflicts (FR, 1996). Gear modification has proven successful in decreasing depredation and bottlenose dolphin mortality caused by entanglement in the blue crab fishery in Florida, in reducing seabird bycatch in coastal gillnet fisheries, and in reducing sea turtle entanglement in shrimp trawlers (Crowder et al., 1994; Melvin et al., 1999; Noke and Odell, 2002;). Our preliminary tests demonstrated that a modification to the outrigger planer will successfully deter bottlenose dolphins from engaging in depredation, without causing a reduction in catch. The deterrence device is made of fishing gear already owned by most fishermen and therefore the cost of the gear modification is minimal.

The deterrence device could prove beneficial in reducing fishery-related injury or mortality of bottlenose dolphins in the king mackerel troll fishery, including harm that may result from retaliatory measures of some fishermen. The 1994 amendments to the Marine Mammal Protection Act of 1972 allow the operator of a fishing vessel to deter a marine mammal from damaging his gear or catch. However, potentially harmful methods, such as guns and seal bombs observed and reported in the Florida king mackerel fishery, are strictly prohibited (FR, 1995). The deterrence device offers an alternative to such illegal measures and their associated harmful consequences. We recommend that the deterrence device be fully tested and, if successful, employed as a strategy to reduce depredation and its adverse effects on both fishermen and bottlenose dolphins.

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We thank two anonymous reviewers who provided suggestions that improved this manuscript. Laura Engleby and the Dolphin Ecology Project provided housing and support that made this study possible. We acknowledge the Edna B. Sussman Fund and the Environmental Internship Fund at Duke University's Nicholas School of the Environment and Earth Science for providing funds to support this research and Steve McCulloch at Harbor Branch Oceanographic Institute for supplying housing on the east coast of Florida. Leigh Torres, Dave Johnston, Danielle Waples, and Kim Urian provided invaluable assistance with this study. We also thank Eric Blankfield who diagramed the fishing gear device. Finally, our appreciation goes to all participating fishermen.

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Reproductive biology, spawning season, and growth of female rex sole (*Glyptocephalus zachirus*) in the Gulf of Alaska

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Abstract—Rex sole (*Glyptocephalus zachirus*) have a wide distribution throughout the North Pacific, ranging from central Baja California to the western Bering Sea. Although rex sole are an important species in the commercial trawl fisheries off the U.S. West Coast, knowledge of their reproductive biology is limited to one study off the Oregon coast where ovaries were analyzed with gross anatomical methods. This study was initiated to determine reproductive and growth parameters specific to rex sole in the Gulf of Alaska (GOA) stock. Female rex sole (n=594) ranging in total length from 166 to 552 mm were collected opportunistically around Kodiak Island, Alaska, from February 2000 to October 2001. All ovaries were analyzed by using standard histological criteria to determine the maturity stage. Year-round sampling of rex sole ovaries confirmed that rex sole are batch spawners and have a protracted spawning season in the GOA that lasts at least eight months, from October to May; the duration of the spawning season and the months of spawning activity are different from those previously estimated.

Female rex sole in the GOA had an estimated length at 50% maturity (ML_{50}) of 352 mm, which is greater than the previously estimated ML_{50} at southern latitudes. The maximum age of collected female rex sole was 29 years, and the estimated age at 50% maturity (MA_{50}) in the GOA was 5.1 years. The von Bertalanffy growth model for rex sole in the GOA was significantly different from the previously estimated model for rex sole off the Oregon coast. This study indicated that there are higher growth rates for rex sole in the GOA than off the Oregon coast and that there are differences in length at maturity and similarity in age at maturity between the two regions.

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Rex sole (*Glyptocephalus zachirus*) have a wide distribution throughout the North Pacific, ranging from central Baja California to the western Bering Sea (Mecklenburg et al., 2002). The rex sole population is made up of several stocks that are managed as four separate units: the U.S. West Coast stock which includes waters off the coasts of California, Oregon, and Washington; the British Columbia stock which is managed separately by the Canadian government; the Gulf of Alaska (GOA) stock; and the Bering Sea stock (Turnock[1]). The U.S. West Coast stock of rex sole provided a steady and stable commercial fishery in California between 1970 and 1989, but landings began to decline in the 1990s (Quirollo and Dewees[2]). Rex sole are managed as part of the "other flatfish" category for both the West Coast stock (Quirollo and Dewees[2]) and the Bering Sea stock (Spencer et al.[3]).

Throughout its range, the largest commercial harvest of rex sole occurs in the GOA where rex sole are one of the major commercial flatfish species. Since 1988, the commercial trawl fishery for flatfish in the GOA has concentrated in the central Gulf on the continental shelf and slope east of Kodiak Island (DiCosimo and Kimball[4]). Development of a management plan for the rex sole fishery in the GOA has undergone several phases. Prior to 1990, all flatfishes in the GOA with the exception of Pacific halibut (*Hippoglossus stenolepis*) were managed as one assemblage. In 1990, four flatfish categories were created for stock assessment: shallow-water complex, deep-water complex (rex sole included), flathead sole (*Hippoglossoides elassodon*), and arrowtooth flounder (*Atheresthes stomias*). In 1993, rex sole were removed from the deep-water complex and managed as a separate species.

In 2003, biomass estimates for rex sole in the Gulf of Alaska totaled 99,950 metric tons (t), and the acceptable biological catch (ABC) was 9466 t (Turnock et al.[5]). Annual commercial landings for GOA rex sole averaged about 3000 t during 1999–2003, approximately 35% of the ABC (Turnock et al.[5]). The low harvest level may be due, in part, to constraints placed on

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the trawl flatfish fishery once the allowed limit of Pacific halibut bycatch is captured (DiCosimo and Kimball[4]).

The life history, reproductive biology, and growth of rex sole were investigated off the Oregon coast from 1969 to 1973 (Hosie and Horton, 1977). Despite the wide geographic range of rex sole, no investigations have occurred elsewhere. Although rex sole in the GOA are managed as a single species unit with species-specific assessments of biomass and ABC estimates, there is no information on length or age at maturity to incorporate into analytical stock assessments. Thus, there is a substantial need for obtaining information on the reproductive biology of rex sole in the GOA for the purpose of stock-specific assessment and management.

To clarify the seasonal maturation dynamics and reproductive biology of female rex sole in the GOA, fish were collected year-round and their ovaries were analyzed by using standard histological techniques. To date, there have been no histological investigations on rex sole maturity (Castillo, 1995). Specific goals of this investigation were to determine the spawning season, length at first maturity, length at 50% maturity (ML_{50}), age at first maturity, and age at 50% maturity (MA_{50}). Additionally, inasmuch as possible, reproductive parameters and growth were compared between female rex sole in the GOA with those off the Oregon coast (data from Hosie and Horton, 1977). Reproductive parameters determined in this study will aid the development of a species-specific assessment of target fishing mortality rates and mature female biomass, yielding a more accurate management model for the GOA stock of rex sole.

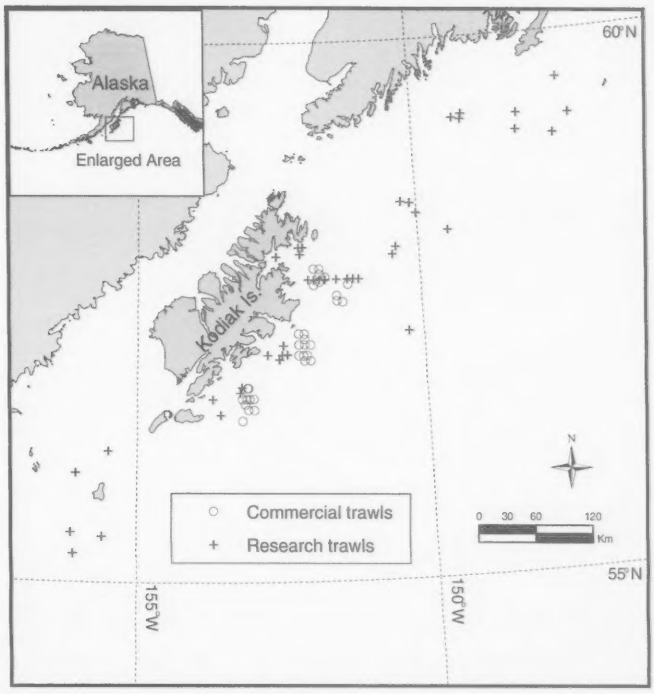

Figure 1

Collections of female rex sole (*Glyptocephalus zachirus*) in the Gulf of Alaska were concentrated around Kodiak Island, Alaska. Samples were obtained from the commercial trawl fishery (denoted by open circles) and from research survey trawls (denoted by crosses).

Materials and methods

Collections

Rex sole were collected from 14 February 2000 to 21 October 2001 in the central GOA (from 55°30′N, 156°00′W to 59°50′N, 147°15′W; Fig. 1). Approximately half (52%) of the samples were collected at fish processing plants in Kodiak, Alaska. The shore-side sampling data were dependent on the timing of the fishery, but allowed for the annual cycle of sexual maturation to be monitored. Shore-side sampling occurred in January, February, April, May, October, November, and December, and samples were obtained from boats that captured rex sole as bycatch while fishing for other species. Although there is no inherent biological difference in rex sole collected by commercial or research trawl, typically samples from the commercial fishery exclude young fish that are below the minimum landing size or escape through the meshes. However, because of the close proximity of the fishing grounds to the town of Kodiak, catches were not sorted at sea and very small rex sole (minimum total length [TL]=172 mm) were brought back to the processing plants where they were obtained for this study. The remaining 48% of samples were collected during research surveys in February, March, June, and July by the National Marine Fisheries Service (NMFS) and the University of Alaska Fairbanks with smaller-meshed trawls in the same waters fished by the commercial fishery.

Samples were stratified by length, so that up to five females per 1-cm length group were obtained each month. For each female, total length (to the nearest mm) and weight (to the nearest 0.1 gram) were measured, both sagittal otoliths were removed, and ovarian maturity was macroscopically staged. Each ovary was removed and weighed separately (to the nearest 0.1 gram). Ovaries were preserved in 10% buffered formalin for 2 months and then transferred to 70% ethanol. All ovaries collected at sea were weighed only after preservation; ovaries collected at processing plants were weighed both when fresh and after preservation.

Sagittal otoliths were removed from each fish, stored in a glycerol and thymol solution, and most (n=557)

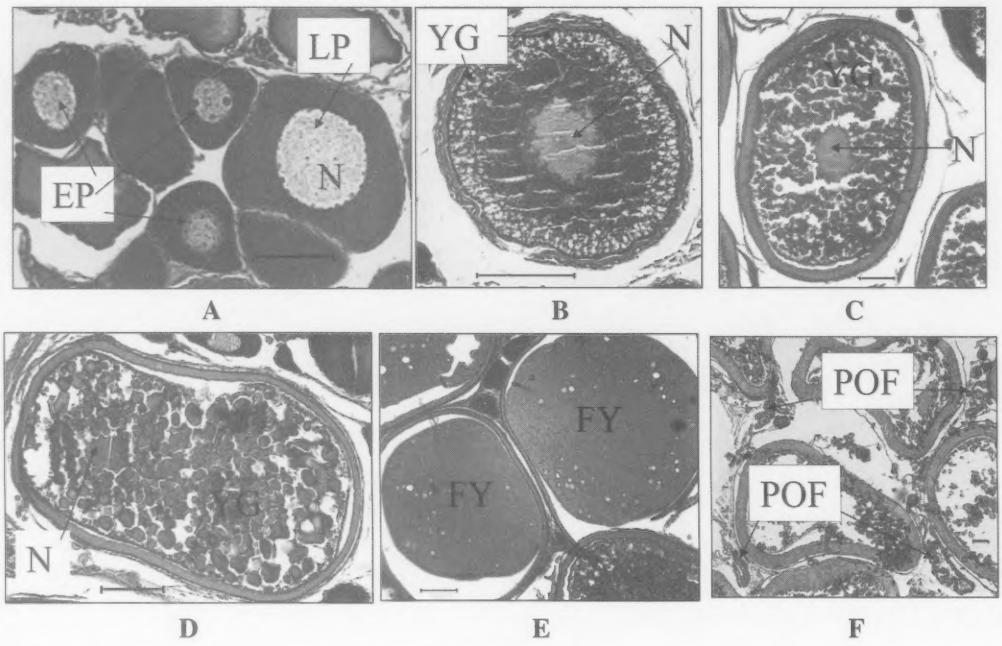

Figure 2

Photomicrographs of histological cross-sections of rex sole (*Glyptocephalus zachirus*) ovaries: (**A**) early perinuclear (EP) oocytes and late perinuclear [EP] oocytes, with a large central nucleus (N), that have not begun vitellogenesis; (**B**) early yolked oocyte beginning vitellogenesis with yolk globules (YG) at periphery of oocyte; (**C**) advanced yolked oocyte; (**D**) migratory-nucleus oocyte; (**E**) hydrated oocytes with fused yolk (FY); (**F**) postovulatory follicles (POFs). Each photomicrograph has a scale bar equal to 0.1 mm.

were analyzed for age determination. The left otolith, or blind-side otolith, was read because it is thicker along the proximal-distal axis, thereby allowing the annuli to be less compressed and easier to differentiate when counted from the core to the otolith edge along the sulcus (Anderl[6]). Otoliths were processed with standard break-and-burn techniques (Beamish and Chilton, 1982). Two experienced readers each read 117 otoliths and had initial agreement of 67%. The magnitude of the initial discrepancies within an age-group ranged from –2 to +3 years for females from age 2 to 18 years. All discrepancies of age estimates were resolved between readers through combined analysis. Once all discrepancies were resolved, the remaining otoliths were analyzed.

Histological analysis

Tissue from the middle portion of the right (ocular-side) ovary was embedded in paraffin Paraplast (McCormick Scientific, St. Louis, Missouri). Serial sections (5–8 microns thick) were prepared and stained with Harris hematoxylin (Sigma Aldrich, St. Louis, MO) followed by eosin counterstain (Sigma Aldrich, St. Louis, MO) (H&E). Each ovary section was examined for the presence or absence of the following oocyte stages (see Fig. 2): oocytes that had not begun vitellogenesis (early perinuclear [EP] and late perinuclear [LP]); oocytes in the first vitellogenic stages (early yolk [EY]); advanced yolked oocytes (AY); oocytes with a migratory-nucleus (MN); unovulated hydrated oocytes (HY); ovulated hydrated oocytes (ova); and postovulatory follicles (POF). During the initial stage of oocyte degeneration (known as alpha [α] atresia) the entire oocyte is resorbed by the hypertrophying granulosa cells of the follicle (Lasker, 1985). Presence of alpha atresia was noted for all histological stages of oocyte development, and the degree of alpha atresia in yolked oocytes was classified as either greater or less than 50% of all yolked oocytes in the ovary. The thickness of the ovarian wall was measured at five or more locations with an ocular micrometer.

Histological classification

Based on histological analysis, spawning categories were created for females (Table 1) according to the clas-

[6] Anderl, D. 2003. Personal commun. Alaska Fisheries Science Center, National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle, WA 98115.

Table 1

Histological criteria for female rex sole (*Glyptocephalus zachirus*) reproductive state and maturity. Active female ovaries contained a sufficient number of advanced yolked oocytes for one spawning. Abbreviations are as follows: migratory-nucleus oocytes (MN), hydrated oocytes (HY), postovulatory follicles (POFs), oocyte stage present (+); oocyte stage absent (○); oocyte stage not considered (–), and either one or both oocyte stages present (>). A postspawning fish has totally spent ovaries.

Ovary activity	Maturity stage	Spawning condition	Unyolked oocytes	Early yolked oocytes	Advanced yolked oocytes	MN or HY oocytes	POFs	>50% yolked atresia	Number of fish in stage
Inactive	Immature	Nonspawning	+	○	○	○	○	–	274
Inactive	Mature	Nonspawning	–	+	○	○	○	–	44
Inactive	Mature	Nonspawning	–	–	+	–	○	+	0
Inactive	Mature	Postspawning	–	–	+	–	+	+	96
Active	Mature	Nonspawning	–	–	+	○	○	○	26
Active	Mature	Spawning	–	–	–	+	○	○	27
Inactive	Mature	Postspawning	–	–	○	○	+	–	14
Active	Mature	Spawning	–	–	>	>	+	○	113
Total									594

sification from Hunter et al. (1992). Females were first classed as active or inactive by using the following criteria. Through histological analysis, ovaries that contained a sufficient number of AY/MN/HY oocytes for one spawning were classed as active. Active females were then classed as either spawning or nonspawning. Ovaries without AY oocytes or with major atresia of AY oocytes were classed as inactive. Inactive females were first classed as nonspawning or postspawning and then inactive nonspawning females were further classed as mature or immature (Table 1). Active spawning females showed evidence of past spawning (POF present) or imminent spawning (MN or HY present), whereas active nonspawning females had no evidence of recent or imminent spawning but were presumed capable of spawning in the near future. Females with ovaries containing oocytes in early stages of vitellogenesis (EY oocytes present) were considered mature but inactive. Immature females had ovaries without vitellogenic oocytes.

The fraction of active females and the fraction of postspawning females was calculated for each month. The start of the spawning season was defined by the first observance of a hydrated oocyte or a POF and the end of the spawning season was defined when the last female with hydrated oocytes was observed. A one-way ANOVA was used to test for differences in the ovary wall thickness of mature females among months. Assumptions of homogeneity of variances and normal distribution of observations were met for the ANOVAs. Bonferroni all-pairwise multiple comparison tests were used after the ANOVAs to test for differences among monthly mean values. Alpha was set at 0.05 for all tests of significance.

To estimate the length and age at which 50% of the female rex sole were mature ($ML_{50}$and MA_{50}), I used the logistic regression model:

$$Pmat = 1 / (1 + e^{a+bL}),$$

where $Pmat$ = the fraction of mature females per 15-mm length-class; and

L = total length in millimeters.

Similarly, for estimating MA_{50},age (in years) was substituted for length in the above equation. In each case, the equation was solved for $Pmat = 0.5$ to obtain the length and age at 50% maturity. The equation for the upper and lower 95% confidence limits around $Pmat$ when $Pmat = 0.5$ was solved to yield 95% confidence limits around $ML_{50}$and MA_{50}. Results were compared with existing length-at-maturity data for female rex sole off the Oregon coast by reconstructing a length-at-maturity logistic regression model from data presented by Hosie and Horton (1977), taking the log transformation of both the GOA and Oregon logistic regression curves to make them linear, and then comparing the slopes of the two lines according to Zar (1999). Direct statistical comparison with existing age-at-maturity data (e.g., the age at 50% maturity, and age at 100% maturity) for female rex sole off Oregon (Hosie and Horton, 1977) was not conducted because Hosie and Horton (1977) did not present standard error or logistic regression equations. Instead, the probability that a specific-size (or specific-age) female rex sole off the coast of Oregon would be considered mature in the GOA was calculated as the fraction of mature GOA females of the specified length divided by the GOA sample size of the specified length (Zar, 1999).

Size and growth

The relationship between weight and length for female rex sole in the GOA was estimated with the equation

$$W = aL^b,$$

where W = the total fish weight in grams; and
L = total length in cm.

This relationship was also determined for ovary-free weight. Because fresh ovarian weights were not measured for samples collected at sea, the fresh weight was estimated from a linear regression between fresh and preserved weights from the samples collected at processing plants. The linear regression OW=1.127 (OW_f)–0.024 was used to convert formalin-preserved ovary weights, OW_f, to estimates of fresh ovary weights, OW (n=446, r^2=0.997, P<0.0001). When fresh and preserved ovary weights differed; fresh ovaries usually weighed more than ovaries preserved in formalin, and the maximum difference between fresh ovaries and formalin-preserved ovaries was 20%.

Parameters of the von Bertalanffy growth model (L_∞, k, and t_0) were estimated for female rex sole in the GOA by using nonlinear least squares regression with the equation

$$L_t = L_\infty (1 - e^{-k(t - t_0)}),$$

where L_t is length at age t.

All length and age data were used for the GOA growth model. Statistical comparison of growth rates for female rex sole in the GOA with those from the Oregon coast were less rigorous because Hosie and Horton (1977) used mean values of length at age to calculate the von Bertalanffy growth model, thereby decreasing the variability in length at age, which was not presented. Therefore, the parameters L_∞, k, and t_0 in the GOA growth model were each statistically compared with the parameters in the Oregon growth model for females age 1–15 years (data from Hosie and Horton, 1977) with three separate Z-tests (Zar, 1999). Alpha was set at 0.05 for all tests of significance.

Results

Maturity

Oocyte development and maturity stage were determined for 594 female rex sole. Histological examination revealed that 46% of the collected females were immature and 54% were mature. Both immature and mature females were collected in every month; however, no fish were sampled in August or September (Table 2). Year-round histological analysis of ovaries confirmed that rex sole are batch spawners, as seen in the presence of POFs, features associated with recent spawning, concurrent with advanced vitellogenic oocytes.

The spawning season of rex sole in the GOA was protracted; postovulatory follicles first appeared in October and hydrated oocytes occurred as late as May, indicating a spawning season that spans at least eight months. Active females were present from October through May and were absent in June and July (Table 2). Mature postspawning females with no healthy AY oocytes first appeared in April and increased in June and July; thus, the spawning season ended in April for some individuals, and by June all rex sole had completed spawning (Fig. 3). The high number of postspawning fish combined with the absence of spawning fish in June and July indicated that the duration of POFs in an ovary was several weeks. Active females had at least one of the following oocytes (AY, MN, or HY) and could have any combination of these advanced stage oocytes, or all three oocyte stages at once. These oocytes were large and stretched the ovary wall quite thin, whereas inactive postspawning females had shrunken ovaries and thicker ovary walls (Maddock and Burton, 1999). In May and July ovary walls in mature females were significantly thicker than in all other months sampled (ANOVA: $F_{9,274}$=28.64, P<0.0001; Fig. 4), corresponding to the high fraction of postspawning females present from May to July (Table 2, Fig. 3).

Female rex sole sampled for length and maturity ranged from 166 to 552 mm TL (Fig. 5). The smallest

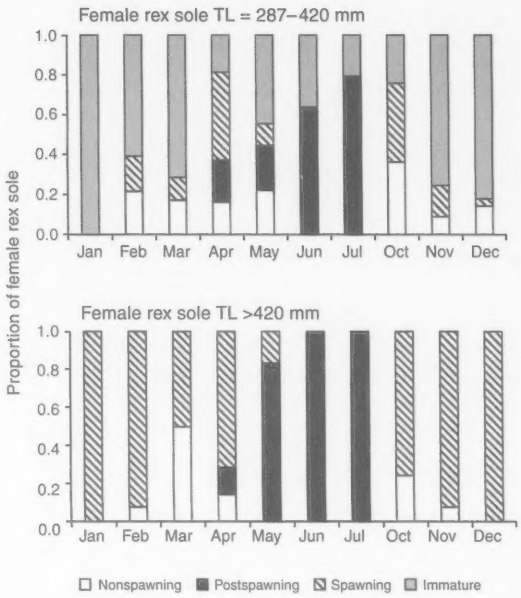

Figure 3

Monthly proportion of female rex sole (*Glyptocephalus zachirus*) maturity stages graphed separately for fish greater than size at first maturity (287–420 mm in upper graph) and fish greater than size at 100% maturity (>420 mm in lower graph). No data were collected in August or September. All mature rex sole were in the postspawning stage in June and July.

Table 2

Numbers of female rex sole (*Glyptocephalus zachirus*) in various histological subclasses, listed by month with years combined. Abbreviations are as follows: postspawning (PS), nonspawning (NS), spawning (S), early yolked oocytes (EY), advanced yolked oocytes (AY), migratory nucleus oocytes (MN), and hydrated oocytes (HY). Mature PS females had ovaries that contained post-ovulatory follicles (POF), and mature S females had ovaries that contained either MN or HY oocytes or AY oocytes combined with POF. The length distribution (minimum, maximum) and the total number of females sampled in each month are given. The percent active females in each month is given, and female rex sole were active from October through May. PS females were present from April to July. No collections were made in August or September.

Ovary activity	Maturity stage	Histological criteria	Jan	Feb	Mar	Apr	May	Jun	Jul	Oct	Nov	Dec	Total
Inactive	Immature	Unyolked oocytes	2	75	33	20	13	14	36	10	41	30	274
	Mature	EY; <50 % atresia	0	13	10	8	2	0	0	6	1	4	44
	Mature–PS	AY; >50 % atresia; POF	0	0	0	9	6	37	44	0	0	0	96
	Mature–PS	AY absent; POF	0	0	0	1	1	0	12	0	0	0	14
Active	Mature–NS	AY; POF absent	0	5	2	0	0	0	0	15	4	0	26
	Mature–S	MN or HY; POF absent	0	0	0	0	0	0	0	23	3	1	27
	Mature–S	AY, MN, or HY; POF present	5	37	10	24	2	0	0	18	16	1	113
Minimum length (mm)				353	166	250	214	215	257	176	267	172	220
Maximum length (mm)				513	529	552	547	460	503	450	476	460	452
Percent active females			71%	32%	22%	39%	8%	0	0	78%	35%	6%	
Percent postspawning females			0	0	0	16%	29%	73%	61%	0	0	0	
Total number sampled			7	130	55	62	24	51	92	72	65	36	594

mature female in the GOA was 287 mm TL. The nonlinear logistic regression model used to determine a length-at-maturity curve for females in the GOA had a very good fit (n=594, r^2=0.994; Fig. 6). The ML_{50} estimate for rex sole in the GOA was 352 mm (95% CI: 344–360 mm; Table 3), and length at 100% maturity was 420 mm (Fig. 5). Female rex sole in the GOA matured at a significantly larger size than off the Oregon coast (slope comparison: $t_{2,57}$=1356, P<0.0001; Fig. 6). Hosie and Horton (1977) estimated the ML_{50} as 24 cm off the Oregon coast, and at this length no GOA rex sole were mature. At the length that 100% of rex sole from Oregon waters were mature (30 cm; Hosie and Horton, 1977), only 15.8% (n=19) were mature in the GOA. The ML_{50} for female rex sole in the GOA was 46% greater than the ML_{50} for Oregon coast stock.

Female rex sole collected in this study ranged in age from 1 to 29 years. The estimated MA_{50} was 5.1 years (95% CI: 4.7–5.5 years) (n=557, r^2=0.988; Table 3, Fig. 7). Minimum age-at-maturity was 3 years, and all females had reached maturity by age 9, with the exception of two slow growing females who were still immature at ages 9 and 10 years (Fig. 5). These results are nearly identical to those obtained in Oregon (MA_{50}=5 yr, 100% mature at 9 years.; Hosie and Horton, 1977).

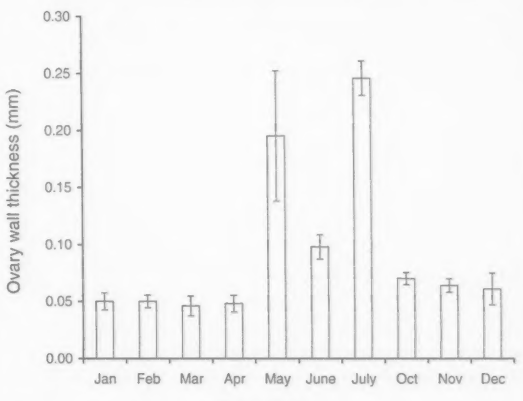

Figure 4

Monthly mean (±1 standard error) ovarian wall thickness (mm) for mature female rex sole (*Glyptocephalus zachirus*). No data were collected in August or September.

Size and growth

Parameters for the weight (g) to total length (cm) relationship for female rex sole in the GOA were

$W=0.000762L^{3.6127}$ (n=573, r^2=0.963, P<0.0001). Parameters for the ovary-free weight to total length (cm) relationship were $W=0.001277L^{3.4680}$ (n=568, r^2=0.969, P<0.0001). Parameters of the von Bertalanffy growth model for female rex sole in the GOA were L_∞=41.824, k=0.388, and t_0=−0.022 (n=556, r^2=0.480, P<0.0001). All GOA parameters of the von Bertalanffy growth model differed from those off the coast of Oregon: L_∞ (Z=8.01, P<0.0001), k (Z=5.61, P<0.0001), and t_0 (Z=2.29, P=0.0110). Female rex sole age 1–15 years grew much more quickly in the GOA than off the Oregon coast (Fig. 8).

Discussion

A representative sample of fish can be challenging to collect during the spawning season, because samples from spawning aggregations may produce disproportionately large numbers of mature fish whereas samples from elsewhere may yield unusually large numbers of immature fish (Sampson and Al-Jufaily, 1999). The combination of samples from commercial trawls and randomly chosen trawls taken on research surveys provide a reasonable representation of the GOA population and are suitable for estimating spawning season, length and age at maturity, and growth rate. Shore-side sampling of the commercial catch enabled the annual cycle of rex sole sexual maturation to be monitored, and although a common problem in obtaining samples from commercial fishing gear is that the size-selectivity of trawls may produce biased estimates of size frequency and size at age (Sampson and Al-Jufaily, 1999), this concern was alleviated because small rex sole (minimum length=172 mm) were collected from processing plants.

One limitation in the sampling effort was that samples could not be obtained in August and September. This raises two concerns. First, the onset of the GOA spawning season was estimated to be October by the presence of POFs in mature ovaries; but, in all probability, it may begin earlier. Second, Hunter et al. (1992) argue that length and age at maturity are best estimated from fish collected prior to the spawning season, because during the spawning season the ovaries of some postspawning females are reabsorbed to the extent that they are indistinguishable from those of immature females. Their estimates of Dover sole (*Microstomus pacificus*) length at maturity from samples taken during the spawning season were 1.6–5.7 cm higher than estimates from samples taken prior to the onset of spawning (Hunter et al., 1992). Given that GOA collections were unavailable prior to the spawning season, estimates of ML_{50} in the present study may have been biased high. However, because 1) all postspawning females had POFs present and 2) there were no females that had atretic yolked oocytes without POFs, it is unlikely that mature females were misclassified as immature in this study.

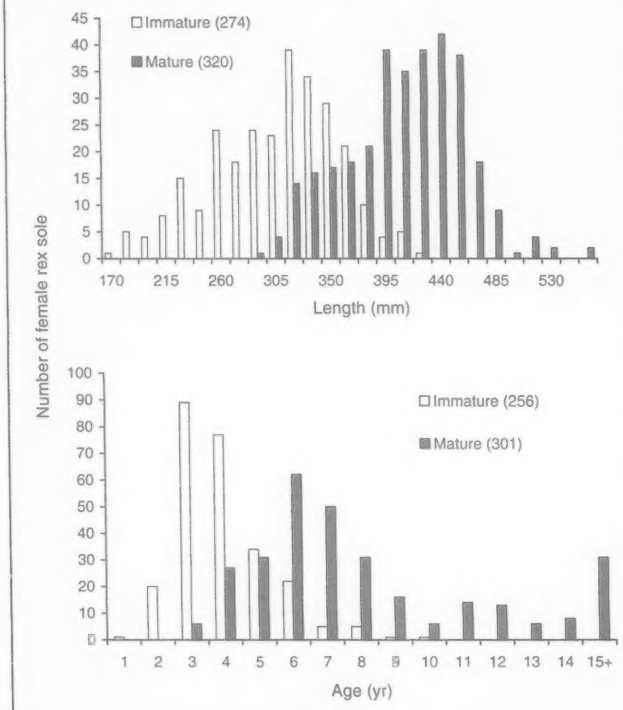

Figure 5

The number of immature and mature female rex sole (*Glyptocephalus zachirus*) by total length (upper graph) and age (lower graph). Sample size is given in parentheses. Lengths are binned at 15-mm increments and "age 15+" includes all females from 15 to 29 years old. Minimum size at maturity occurred in a fish with total length of 287 mm, and minimum age at maturity occurred at 3 years.

Spawning season

The spawning season for the population of female rex sole in the GOA ends in May and appears to commence in October, although it may begin earlier (see above). Castillo (1995) estimated the spawning season for rex sole in the GOA lasts from April through September, which differs markedly from results in the present study which are based on year-round histological examination of ovaries. Castillo (1995) based his estimation on the seasonal occurrence of rex sole larvae near Kodiak Island (Kendall and Dunn, 1985) rather than on collections of adult rex sole in spawning condition. Because rex sole larvae attain an exceptionally large size (up to 89 mm standard length) and have a prolonged pelagic life of

Table 3

Logistic regression model for female rex sole (*Glyptocephalus zachirus*) in the Gulf of Alaska: final maturity thresholds, length and age at 50% maturity (ML_{50} and MA_{50}), sample size (n), model parameter estimates, and the model r^2.

Variable	ML_{50}/MA_{50}	95% CI	n	a	SE	b	SE	Model r^2
Length (mm)	351.7	343.7–359.7	594	13.79	0.77	−0.0392	0.0022	0.994
Age (years)	5.1	4.7–5.5	557	5.29	0.45	−1.0375	0.0854	0.988

at least 12 months (Pearcy et al., 1977), the indeterminate pelagic larval phase may have confounded Castillo's (1995) estimates.

Fish may adjust their spawning season to synchronize larval hatching date with the season that is most favorable for larval feeding (Qasim, 1956). Because primary production at northern latitudes is restricted to a short, intense period during early summer, fishes at higher latitudes often delay and shorten their breeding season as an adaptation to synchronize the feeding of fish larvae with the zooplankton bloom (references in Qasim, 1956; Castillo, 1995). However, rex sole in the GOA spawn earlier in the year and for a longer duration than those off the Oregon coast, which spawn from January to June (Hosie and Horton, 1977). Hence, rex sole do not fit the typical pattern of geographic variation found in other pleuronectids, such as English sole (*Pleuronectes vetulus*; Kruse and Tyler, 1983; Sampson and Al-Jufaily, 1999), Dover sole (Abookire and Macewicz, 2003), and yellowtail flounder (*Limanda ferruginea*; Zamarro, 1991).

Maturity and growth

Size and age at sexual maturity are two important parameters of fish stock assessment models used to estimate spawning biomass and annual catch quotas, but these parameters may vary throughout the geographic distribution of a species (Roff, 1981; Nichol, 1997; Bromley, 2000) and can be influenced by food availability (Castillo, 1995; Sampson and Al-Jufaily, 1999), oceanographic conditions (Kruse and Tyler, 1983; Brodziak and Mikus, 2000), or population size (Morgan and Colbourne, 1999). Along the west coast of North America both English sole (Sampson and Al-Jufaily, 1999) and Dover sole (Brodziak and Mikus, 2000; Abookire and Macewicz, 2003) exhibit geographic variation in length at maturity and growth.

There is some indication that female rex sole mature at a smaller size in the southern portion of their range: off San Francisco, California, females were fully mature at 22.8 cm (in Hosie and Horton, 1977), and off the Oregon coast ML_{50} was 24 cm (Hosie and Horton,

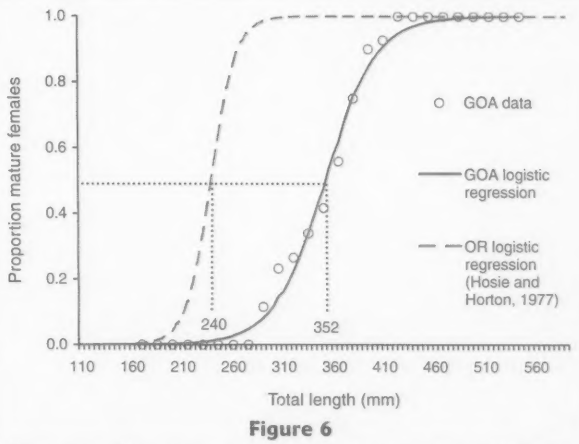

Figure 6

Proportion of female rex sole (*Glyptocephalus zachirus*) that were sexually mature in the Gulf of Alaska (GOA) as a function of total length (mm). Data points along the GOA curve represent the proportion of mature females in each 15-mm length-class interval. Logistic model parameter estimates are listed in Table 3. The dashed line denotes the length at which 50% of females are mature, and the actual size (mm) of ML_{50} is given. A maturity curve for female rex sole off the Oregon (OR) coast (from Hosie and Horton, 1977) is graphed for comparison. Female rex sole in the GOA mature at a significantly larger size than off the Oregon coast ($P<0.0001$).

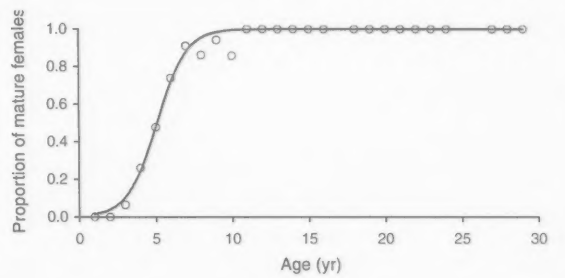

Figure 7

Proportion of female rex sole (*Glyptocephalus zachirus*) in the Gulf of Alaska that were sexually mature as a function of age (years). Datapoints along the curve represent females grouped in intervals of one year. Logistic model parameter estimates are listed in Table 3.

1977). Correspondingly, I found the ML_{50} in the GOA (35 cm) was 46% greater than that off the Oregon coast. Although there is a possibility that rex sole ML_{50} in the GOA was overestimated because sampling did not occur prior to the onset of spawning, the bias cited by Hunter et al. (1992) was relatively small and can not fully account for the 11 cm difference in ML_{50} between the GOA and Oregon. However, some caution must be exercised when maturity is compared between the GOA and Oregon (Hosie and Horton, 1977) because about 25 years elapsed between studies and different criteria were used to classify fish as mature.

Differences in the histological criteria used to define mature individuals and reliance solely on gross anatomical methods can lead to a misclassification of maturity and produce differences in estimates of ML_{50} (Hunter et al., 1992; Zimmermann, 1997). In a comparison of histological and gross anatomical methods, Hunter et al. (1992) found 1% of active female Dover sole were misclassified as inactive and 12% were visually classified as having advanced yolked oocytes and believed capable of spawning, whereas histological analysis indicated that they were inactive and future spawning was unlikely. Likewise, macroscopic examination of arrowtooth flounder misclassified 18.4% of maturing or spent females as immature and 4.4% of immature females as spent (Zimmermann, 1997). Unfortunately, in the only previous investigation on rex sole maturity, Hosie and Horton (1977) limited their analysis of ovaries to macroscopic staging. However, the enormous differences in ML_{50} between the GOA stock and the West Coast stock off Oregon likely stem from biological differences between stocks rather than from inconsistent methods used in the two studies. This interpretation is consistent with the dramatic difference in length at age between the two areas (Fig. 8) that was demonstrated in this study.

Given that Hosie and Horton (1977) used the otolith-surface aging technique to analyze rex sole otoliths, they may have underestimated ages and thereby biased their estimates of both age at maturity and growth rates. However, the tendency to underestimate age with the otolith-surface aging technique is greater for older fish where the outer edges of the otolith are worn (Anderl[7]). Surface analysis of several GOA rex sole otoliths revealed that, although break and burn is the preferred technique for aging rex sole otoliths, it is possible, depending on the clarity of the annular pattern, to age females less than 10 years old accurately by using otolith surfaces (Anderl[7]). Because the ages at 50% and 100% maturity off the Oregon coast were 5 and 9 years old, respectively (Hosie and Horton, 1977), there is a lower potential for bias caused by the surface aging technique because fish were <10 years old. Although these different aging methods may limit comparisons of age at maturity, the similarity in age at maturity between the GOA and Oregon is strongly indicated. Additionally, because the length-at-age data presented in growth curves from Oregon were only for rex sole <15 years old (Hosie and Horton, 1977), and a difference in growth is evident at young ages (Fig. 8), it seems unlikely that potential bias from otolith-surface aging methods—rather than from biological differences between stocks—could account for the markedly lower growth rate of Oregon rex sole. To be sure, it would be useful for future research to compare the reproductive biology and growth data of female rex sole in the GOA with a current study off the Oregon coast that employed similar aging techniques and histological criteria for maturity to determine if the distinct differences found in the GOA stock (i.e., larger size at maturity, similar age at maturity, faster growth rate) persist.

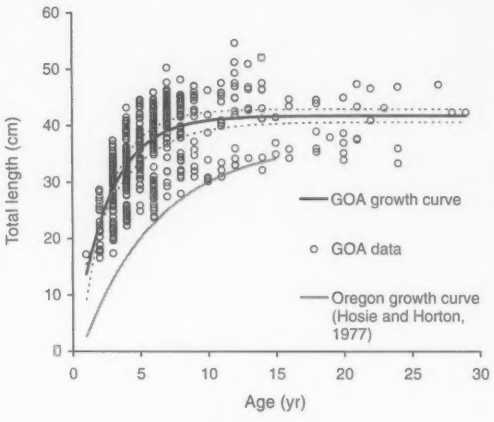

Figure 8

The von Bertalanffy growth curve with 95% confidence limits for female rex sole (*Glyptocephalus zachirus*) in the Gulf of Alaska. Parameters of the Gulf of Alaska growth model were $L_\infty = 41.82$, $k = 0.388$, and $t_0 = -0.022$. For comparison, the growth curve for age 1–15 female rex sole off the Oregon coast is graphed with data from Hosie and Horton (1977).

Acknowledgments

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[7] Anderl, D. 2004. Personal commun. Alaska Fisheries Science Center, National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle, WA 98115.

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Abstract—The contribution of the no-take marine reserve at Apo Island, Philippines, to local fishery yield through "spillover" (net export of adult fish) was estimated. Spatial patterns of fishing effort, yield, and catch rates around Apo Island were documented daily in 2003–2004. Catch rates were higher near the reserve (by a factor of 1.1 to 2.0), but fishing effort was often lowest there. Higher catch rates near the reserve were more likely due to spillover than to low fishing intensity. Lower fishing effort near the reserve may have been due to 1) weather patterns, 2) traditional importance of other fishing grounds, 3) high variability in catch rates, 4) lower market value of target species, and 5) social pressures. The yield taken near the reserve was only 10% of the total yield, but the actual spillover contribution was probably much less than this. This study is one of the few to estimate the spillover contribution to overall yield and to document the responses of fishermen to spillover.

How much does the fishery at Apo Island benefit from spillover of adult fish from the adjacent marine reserve?

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No-take marine reserves (areas closed to fishing) are now often established with an objective of sustaining or enhancing fisheries (Gell and Roberts, 2003). Reserves could achieve such objectives by eventually becoming net exporters of adult biomass, defined as "spillover," and by providing net larval export, known as the "recruitment effect" (Russ, 2002). Fisheries will probably benefit from spillover in a minor way only. Theoretical studies have indicated that potential fishery yield (yield per recruit) from spillover would be insignificant, if any yield at all, except when stock abundance outside reserves is very low due to high fishing mortality (Polacheck, 1990; Russ et al., 1992; DeMartini, 1993). Thus, potential gains from spillover are predicted to be only moderate. There seems to be general agreement that the more important fishery enhancement effect of reserves would be due to net larval export (Carr and Reed, 1993; Russ, 2002). However, the establishment of reserves, particularly in developing countries, requires strong support from local stakeholders, especially fishermen (Russ and Alcala, 1996; Galal et al., 2002). There is a concern that, in some cases, support for reserves may be difficult to obtain on the pretext of enhanced fisheries through increased recruitment (Russ and Alcala, 1996). Net larval export may seem less convincing to fishermen because of the broad spatial scale (tens to hundreds of kilometers) at which it will probably occur (Russ and Alcala, 1996; Russ, 2002). Yields from spillover, although probably small, may play a critical role in convincing fishermen to support establishment and maintenance of reserves (Russ and Alcala, 1996). For some fishermen, adult fish "spilling-over" from reserves, especially in the case of larger fish, will appear to be a more direct and tangible benefit than larvae recruiting to fishing grounds from distant reserves. Thus, spillover may have a substantial positive psychological effect on the attitudes of fishermen toward reserves.

However, few empirical studies have quantified the effects of spillover on fishery yields, nor the responses of fishermen to spillover, perhaps because some advocates of reserves are sometimes overly optimistic about the potential benefits of spillover. Two studies in one location in Kenya showed that after several years of reserve protection, spillover was not enough to compensate for reduction of total yield due to the creation of a large no-take reserve (McClanahan and Kaunda-Arara, 1996; McClanahan and Mangi, 2000). The reserve, Mombasa Marine Park, took away 50–60% (~6–8 km^2) of the total fishing area. In this case the reserve probably occupied too large an area to supplement total fishery yield substantially (McClanahan and Mangi, 2000). However, in other countries, no-take reserves as large as Mombasa

Marine Park are rare. In the Philippines, for example, reserves that are created with fishery enhancement as a major goal are typically small (<1 km^2 of reef area) and occupy ≤25% of the available local fishing area (Alino et al., 2002). To date, only two studies of Philippine reserves, Sumilon and Apo (~25% and ~10% respectively of fishing area are no-take reserves), have shown persuasively that spillover yield may affect total fishery yield (Alcala and Russ, 1990; Russ et al., 2004, Alcala et al., 2005). In both cases, however, the magnitude of actual spillover yield was unclear (Russ et al., 2004, Alcala et al., 2005). On the other hand, two studies, one in St. Lucia (Roberts et al., 2001) and one in Egypt (Galal et al., 2002), demonstrated that catch rates of fishermen increased several years after the creation of networks of reserves. It was argued in these studies that the reserves increased total fishery yield because catch rates improved but fishing effort remained constant. However, these studies provided no information on total fishery yield, precluding estimation of the magnitude of spillover benefits. More empirical studies are needed to provide assessment of potential spillover effects on adjacent fisheries.

Besides available fishing area, the total fishery yield for a given location will be determined by fishing intensity (Hilborn and Walters, 1992). In addition, theoretical studies indicate that spillover yield will be a function of reserve size, fishing mortality rate, and demographic parameters of target species, particularly movement rates (Polacheck, 1990; Russ et al. 1992; DeMartini, 1993). However, the actual contribution of spillover to total yield will be determined by fishing intensity adjacent to reserves. Indeed it has been suggested that the "first" sign of spillover is the sight of fishermen fishing close to reserve boundaries (Gell and Roberts, 2003). This phenomenon would occur presumably in response to higher catch rates near than far from reserves. Spillover is predicted to produce a pattern of higher abundance of target species outside but close to reserve boundaries, but lower abundance farther away (Rakitin and Kramer, 1996; Kramer and Chapman, 1999). Decreasing catch rates (an index of abundance) away from reserve boundaries have been demonstrated by experimental trap fishing outside one reserve in Barbados and one reserve in Kenya (Rakitin and Kramer, 1996; McClanahan and Mangi, 2000). Also, monitoring studies of reserves in Kenya and the Philippines have shown that catch rates of fishermen were higher closer to reserve boundaries than farther away (McClanahan and Kaunda-Arara, 1996; McClanahan and Mangi, 2000; Russ et al., 2003, 2004). In New Zealand, large catches of lobsters were found to be more common closer to Leigh Marine Reserve than farther away (Kelly et al., 2002). However, it is less clear if fishermen tend to concentrate more effort adjacent to reserves when spillover may be present. Some studies suggest that fishermen may do so (McClanahan and Kaunda-Arara, 1996; McClanahan and Mangi, 2000), whereas other studies indicate that fishermen do not (Russ et al., 2003; Wilcox and Pomeroy, 2003). Some of the evidence for fishermen preferentially fishing near reserves is anecdotal (Gell and Roberts[1]). Nevertheless, it is important to stress that intense fishing near the reserve may have the effect of eventually reducing catch rates there (McClanahan and Mangi, 2000).

Fishing effort may not necessarily track the spatial distribution of fish abundance. Fishermen may not favor fishing adjacent to reserves even if catch rates there are higher. Catch rates alone may not explain the spatial distribution of fishing effort, because decisions by fishermen on where to fish are usually aimed at making a profit. Hence, decisions may be influenced by fishing costs, such as fuel or time used traveling to fishing areas (Hilborn and Walters, 1992). These costs will be related to the distance of fishing grounds from home ports or residences of fishermen (e.g., Wilcox and Pomeroy, 2003). If such costs are negligible, then fishing effort may reflect the spatial pattern of catch rates, provided that fishermen have ample information on the latter. However, this situation may be unlikely if fishermen keep information about productive areas to themselves. Furthermore, the strategies of fishermen may become highly complex in fisheries that employ a variety of fishing gears and target a multitude of species (Hilborn and Walters, 1992). This is likely to be particularly true of coral reef fisheries in developing countries (Munro, 1996). Spatial distribution of fishing effort in such fisheries may also depend upon the differential value of target species. In addition, other factors that are unrelated to income may also influence the spatial pattern of fishing effort. These include weather conditions and social factors, such as local traditions or agreements among stakeholders and managers (Wilcox and Pomeroy, 2003). Consideration of the behavior of fishermen in relation to reserves may help determine if reserves are achieving their goal of improving fishery yields through spillover. Successful use of reserves to enhance fisheries would require a case by case understanding of the spatial structure of impacted fisheries, ecosystems, and human communities (Hilborn et al., 2004).

The objective of this study was to estimate the upper limit of the spillover contribution of the no-take reserve at Apo Island, Philippines to the local fishery yield. The reserve at Apo Island has been protected for over 20 years (since 1982), and there is evidence to suggest that spillover is present (Russ and Alcala, 1996; Russ et al., 2003, 2004; Alcala et al., 2005). However, previous studies indicate that access by fishermen to productive areas far from the reserve during favorable weather influences the local fishery yield considerably (White and Savina, 1987; Bellwood, 1988). In the present study, daily fishing effort and yield were documented for eight months covering two monsoonal seasons. Spatial and temporal patterns of fishing effort, yield (biomass and value), and catch rates were examined among fishing

[1] Gell, F., and C. M. Roberts. 2002. Unpubl. report. The fishery effects of marine reserves and fishery closures, 89 p. WWF-US, 1250 24th Street. NW, Washington D.C. 20037.

grounds around Apo island and within a few hundred meters of reserve boundaries.

Materials and methods

Study site

Apo Island (9°4′N, 123°17′E) is located in the central Philippines, about 7 km southeast of the large island of Negros (Fig. 1). It is a small volcanic island with a fringing reef area of 1.06 km^2 to the 60-m isobath (0.54 km^2 to the 20-m isobath). The island is inhabited by a community of about 700 permanent residents. The traditional source of income for the community is fisheries. At present, about 100 residents are full-time or part-time fishermen who use hook and line, gill nets, spear guns, and fish traps, and target at least 60 species of reef fishes, nonreef fishes, and some invertebrates. The majority of local fishermen sell their catch to resident fish buyers on Apo Island. Fish buyers, in turn, bring the catch to Negros to sell in Malatapay town or Dumaguete City.

In 1982, a ~450 m long no-take reserve (sanctuary) was established informally by the local community on the southeastern side of Apo Island (Fig. 1). This reserve occupies approximately 10% of the fringing reef area to the 60-m isobath (about 13% to the 20-m isobath). The local community has effectively enforced protection of the no-take reserve since 1982 (Russ and Alcala, 1999). In 1985–86, the community formally approved a marine management plan that incorporated the no-take reserve (Russ and Alcala, 1999; White et al., 2002). The management plan also prohibited destructive fishing methods (e.g., dynamite fishing and muro-ami drive-net fishing) and spear fishing with SCUBA. Compliance by local fishermen and visitors with these regulations has been generally good. Development of local tourism enterprises has been encouraged by the Marine Management Plan. In the early to mid-1990s, two small resorts that could accommodate recreational SCUBA divers were established on Apo Island. Recently, the local community implemented collection of fees for diving in the no-take reserve and at dive sites around the island.

Apo Island is influenced by a northerly mainstream current that is present for most of the year (Fig. 1). This current presumably carries the food supporting planktivorous fishes (e.g., Acanthuridae and Caesionidae) that are abundant on the northern side of the island. Predatory fishes such as Carangidae are also common in this area. Apo Island is exposed to both the NE and SW monsoons (Fig. 1). Local fishermen tend to fish the northern side of the island during the SW monsoon (June to September) and interim calm months (April, May, and October; Bellwood, 1988). However, fishing intensity on the northern side of the island may be reduced during the NE monsoon (November to March; Bellwood, 1988).

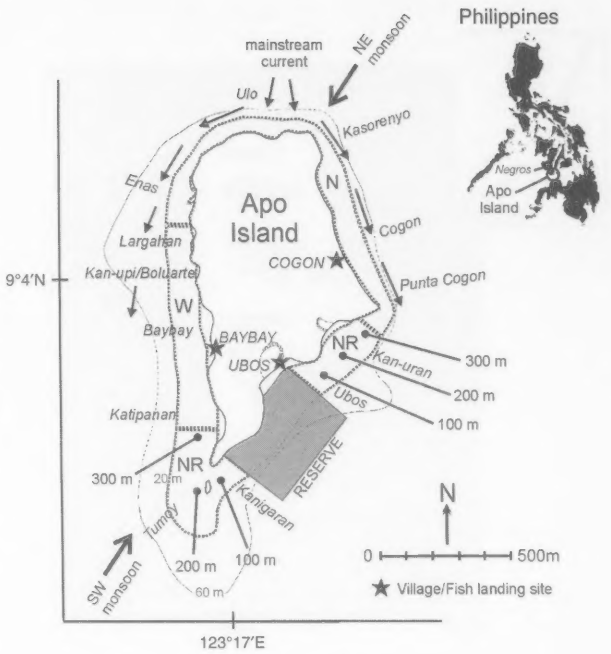

Figure 1

Apo Island, central Philippines, showing the no-take reserve (shaded). Names of fishing grounds around the island are italicized. Fishing grounds were grouped into "northern fishing grounds" (N), "western fishing grounds" (W), and "fishing grounds near Apo Reserve" (NR). The reef area of each of the fishing grounds is outlined (0–20 m isobath). Within the fishing grounds near Apo Reserve, the approximate positions of marker buoys used to indicate distance from either the northern or southern boundary of the reserve are shown. The major fish landing sites were at Baybay, Ubos, and Cogon villages (stars). Large arrows indicate the direction of the monsoons. Smaller arrows indicate direction of the mainstream current.

Data collection

The catches of fishermen residing at Apo Island were recorded daily from 22 July 2003 to 29 February 2004. Records were kept by three fish buyers, one buyer at each of the three major fish landing sites (the houses of the fish buyers) on the island, in Baybay, Ubos, and Cogon villages (Fig. 1). The fish buyers recorded the local names and weights of each species or family of fish that contributed to the catch sold by each fishermen. Catches were weighed on market scales accurate to 0.1 kg. The value of the catch sold by fishermen was estimated by multiplying the weight of each species by its average market price per kilogram in 2003, in Philippine Pesos (PHP). In addition, a resident research assistant (A. Candido) and one of the fish buyers (M. Aldeon) collected information from fishermen at each of the three villages through interviews every few days or weekly. The following information was gathered from fishermen:

fishing grounds visited, names and number of fishers, date and times when fishing started and finished, fishing gear used, and composition and weights of catches (verified from records of fish buyers). Interviewers were able to determine precisely where fishing was conducted because the names and locations of fishing grounds around Apo Island are common knowledge to local people (Fig. 1). However, if fishing was done near Apo Reserve (e.g., at Katipanan, Tumoy, Kanigaran, Ubos, and Kan-uran; Fig. 1), fishermen were also asked to estimate how far away they were from the boundaries of the reserve. Color-coded marker buoys, which fishermen could locate and identify easily while fishing, indicated approximate distances from reserve boundaries. These buoys were moored permanently at 100 m (blue), 200 m (red), and 300 m (yellow) from each of the northern and southern boundaries of Apo Reserve (Fig.1). The buoys were installed with the aid of a GPS receiver and fishermen were informed about them one week before the study started.

Data were collected from 80 full-time and part-time resident fishermen (Baybay–16, Ubos–47, Cogon–17). This group comprised 70–80% of all fishermen at Apo Island. The information in the present study probably reflects accurately the actual patterns of fishing effort and yield of the local market-oriented fishery. The majority of fishermen at Apo Island sell their catch to fish buyers at each of the three fish landing sites monitored (Maypa et al., 2002). The fish buyers usually purchased their fish from a group of "loyal" fishermen. Also, most fishermen live close to the houses of the fish buyers (landing sites). Thus, interviewers were able to collect data from fishermen regularly. Fishing effort and yield data were not adjusted to account for all resident fishermen (i.e., any fishermen not included in interviews).

However, data were not obtained from the following: 1) catch sold to part-time fish buyers on the island, 2) catch sold directly to the main island of Negros, 3) fishermen visiting from Negros, 4) catch sold dried, and 5) catch brought directly to homes for consumption. Items 1–4 are probably minor contributors to the total marketed yield. Maypa et al. (2002) surveyed the same fish landing sites monitored in the present study and estimated that only 10% of the total marketed yield (presumably from items 1–4) did not pass through the three major fish landing sites. On the other hand, yield from subsistence fishing (item 5) may be comparable in quantity to the marketed yield (White and Savina, 1987), but lower in monetary value. It is unlikely, however, that data on fishing effort collected in this study would differ much from data on subsistence fishing. It seemed common that fishermen went to sea to catch fish both to sell and keep for personal consumption.

Data analysis

Targeted species were classified into five groups according to Bellwood (1988): reef-associated species (Carangidae and Sphyraenidae), reef planktivores (Acanthuridae, Caesionidae, and Pomacentridae), reef species (mainly Lutjanidae, Lethrinidae, Scaridae, Serranidae, Kyphosidae, and octopus), open water species (Belonidae, Elopidae, and Scombridae), and off-reef species (Lutjanidae). Fishing grounds were classified into three groups: the northern fishing grounds (Enas, Ulo, Kasorenyo, Cogon, Punta Cogon), the western fishing grounds (Largahan, Kan-upi/Boluarte, Baybay, Katipanan), and the fishing grounds near Apo Reserve (Tumoy, Kanigaran, Ubos, Kan-uran) (Fig.1). Data were included in the third group if fishing was done ≤300 m from reserve boundaries. These three fishing grounds had roughly similar surface areas to the 20-m isobath (northern fishing grounds, 17.3 ha; western fishing grounds, 14.3 ha; fishing grounds near Apo Reserve, 18.9 ha). It was assumed that most fishing was done within or just outside the reef area enclosed by the 0- and 20-m isobaths (Fig. 1). In addition, data for the fishing grounds near Apo Reserve were classified into the following categories of distance from reserve boundaries: 0–100 m, 100–200 m, and 200–300 m.

Interviews allowed collection of fishing effort data even when fishermen returned from trips without catching anything (i.e., fishermen who used hook and line, gill nets, and spear guns). On average, about 20% of total fishing trips (or 23% of total fishing effort in person hours) returned with no catches. This figure varied considerably according to fishing gear (hook and line: 48%, gill net: 3%, spear gun: 7%) and months. However, fishing effort data for trips with zero catch were collected only beginning in September. Hence, the recorded fishing effort (in person hours) in July and August was adjusted by adding a correction factor in order to account for fishing trips with no catches. Correction factors were calculated from the equation

$$EC = [ER \times (EZ / ET)] / [1 - (EZ / ET)], \quad (1)$$

where EC and ER = the correction factor (expressed in person hours) and recorded monthly fishing effort, respectively, for July or August; and
EZ and ET = the total fishing effort with zero catch and the total fishing effort, respectively, in September.

Values for September were used because this month is within the same season as July and August (SW monsoon). Correction factors were calculated per gear (hook and line, gill net, and spear gun) and per group of fishing grounds. However, prior to adjustment, the recorded monthly fishing effort for July was multiplied by three to obtain an estimate for a 30-day period. The yield for July was also multiplied by three to obtain a 30-day yield estimate. Catch per unit of effort (CPUE, in kg/person per hour for each month was calculated by taking the average CPUE of all individual fishing trips made in a given month. Monthly CPUE was calculated per gear, per group of fishing grounds, and per distance from reserve boundaries (0–100, 100–200, and 200–300 m). July and August CPUE were adjusted

to account for fishing trips with zero catch, by adding correction factors (expressed in number of fishing trips) calculated by using Equation 1. Hence, correction factors were the number of fishing trips with zero CPUE. Income per unit of effort (IPUE) was used as an indicator of economic value among fishing grounds. This was calculated in the same manner as CPUE, expressed in PHP/person per hour. IPUE for July and August were adjusted in the same manner as CPUE.

ANOVA was used to determine how fishing effort for each of the three principal gear (hook and line, gill net, and spear gun [fish traps were rarely used]) varied according to seasons (SW monsoon and interim period vs. NE monsoon) and fishing grounds (northern, western, and near Apo Reserve). ANOVA was also used to determine how CPUE or IPUE varied according to fishing grounds and the three principal fishing gear and how CPUE varied according to distance from reserve boundaries (0–100, 100–200, 200–300, and >300 m) and the three principal fishing gears. Monthly estimates of each variate of interest were used as replicates in each ANOVA. Variates were transformed (log [x+1] or square root [x+1]) to satisfy ANOVA assumptions. Tukey's test (Zar, 1999) was used in all *post hoc* analyses.

Two sets of indicators of relative economic value were used besides IPUE. The first was the frequency of capturing high-value species, and the frequency of landing a high yield of such species, expressed in number of fishing trips. This was summarized per species group and per fishing ground. High-value species were those with the highest, or the first and second highest, price per kg within species groups. Determination of a "high yield" within high-value species depended upon the average sizes of individuals within species groups, and whether species were usually landed as individuals or as groups. The following were considered high yield for high-value species: reef associated species (Carangidae, 3 spp.), ≥7.0 kg; reef planktivores (Caesionidae, 2 spp.), ≥3.0 kg; reef species (Serranidae, 3 spp., Lutjanidae, 7 spp., Lethrinidae, 2 spp.), ≥2.0 kg; open water species (Scombridae, 2 spp.), ≥7.0 kg; off-reef species (Lutjanidae, 1 sp.), ≥2.0 kg. The second indicator of economic value was the probability of capturing high-value species, and the probability of landing a high yield of such species, calculated on the basis of one fishing trip. This was calculated by dividing the frequencies (the first set of indicators) by the total number of fishing trips that used appropriate fishing gear to capture high-value species. Probabilities were calculated per species group and per fishing ground. Yield from traps were excluded in this analysis.

Results

Seasonal patterns of fishing effort and catch composition among fishing grounds

Hook-and-line fishing The majority of hook-and-line effort (73–98%) was made on the northern fishing grounds from July to December (Fig. 2A). However, during this period, hook-and-line fishing on the northern fishing grounds declined steadily (from 2302 to 50 person hours/month). It remained at low levels from January to February (35–173 person hours/month). Hook-and-line effort on the northern fishing grounds averaged 1015 ±342 (SE) person hours/month. The total hook-and-line yield from this area was 3549 kg (Table 1), dominated by reef-associated species (57%, mainly Carangidae) and reef planktivores (24%, mainly *Naso* spp.). Hook-and-line effort on the western fishing grounds was much lower, averaging 56 ±22 person hours/month (Fig. 2A). However, in January and February, hook-and-line effort on the western fishing grounds increased slightly (52–93 person hours/month). During this period, 38–62% of the total hook and line effort was made on the western fishing grounds, targeting an off-reef species (*Aphareus furca* (Lacepede) [Lutjanidae]). The total hook-and-line yield from the western fishing grounds was only 202 kg (Table 1), dominated by off-reef species (37%). Hook-and-line effort on the fishing grounds near Apo Reserve was the lowest among fishing grounds, averaging 33 ±9 person hours/month (Fig. 2A). It did not exhibit distinct seasonal patterns. The total hook-and-line yield near the reserve was only 166 kg (Table 1), dominated by reef species (38%, mainly octopus).

Hook-and-line effort (square root [x+1] transformed) differed significantly between seasons (ANOVA, $F_{1,18}$= 13.14, P=0.002) and among fishing grounds (ANOVA, $F_{2,18}$= 35.08, P<0.001). The season by fishing ground interaction was significant (ANOVA, $F_{2,18}$=16.34, P<0.001). During the SW monsoon and interim period (July to October), hook-and-line effort on the northern fishing grounds was significantly higher than on the western fishing grounds (Tukey's test, $q_{3,18}$=12.45, P<0.001) and on the fishing grounds near Apo Reserve (Tukey's test, $q_{3,18}$=11.84, P<0.001). During the NE monsoon (November to February), hook-and-line effort did not differ significantly among fishing grounds. Hook- and-line effort on the northern fishing grounds was significantly higher during the SW monsoon and interim period (July to October) than during the NE monsoon (November to February) (Tukey's test, $q_{2,18}$=9.48, P<0.001). No significant differences in hook-and-line effort between seasons were found on the western fishing grounds and on the fishing grounds near Apo Reserve.

Gillnet fishing Gillnet fishing occurred mostly on the northern fishing grounds (194–466 person hours/month) from July to October (Fig. 2B). Gillnet effort on the northern fishing grounds averaged 268 ±44 person hours/month. The total gillnet yield from this area was 724 kg (Table 1), dominated by reef planktivores (76%, mainly Caesionidae). Beginning in November, gillnet effort shifted from the northern to the western fishing grounds. Gillnet effort on the western fishing grounds increased dramatically from zero in July, to 545 person hours/month in November (Fig. 2B). From November to February, the western fishing grounds accounted for 36–63% of the total gillnet effort. Gillnet effort on

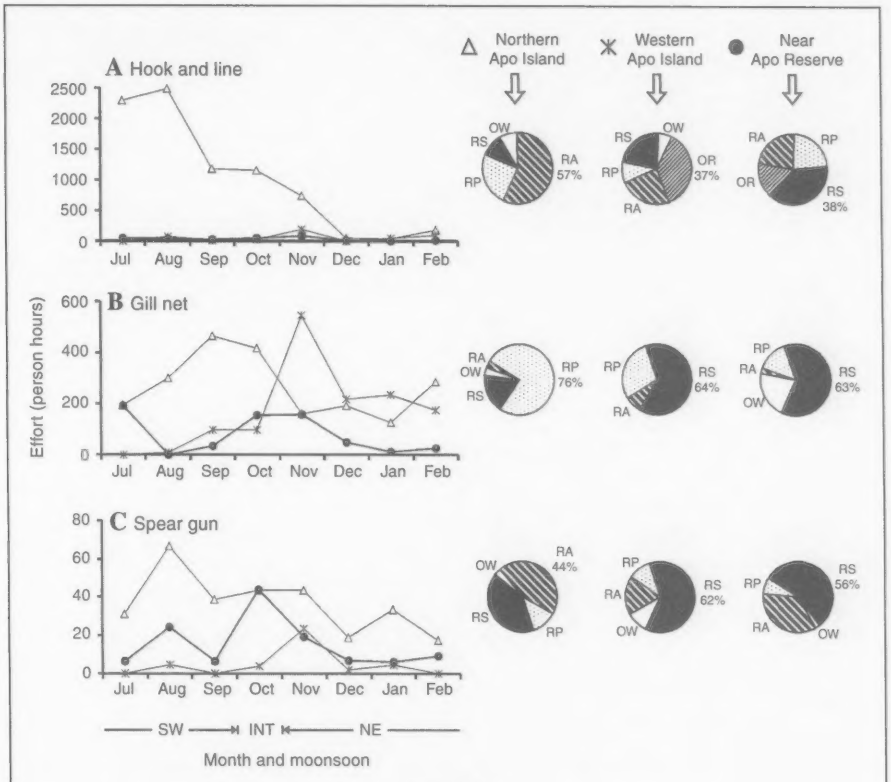

Figure 2

Seasonal trends in fishing effort (left-hand side) and composition of yield (right-hand side) for (**A**) hook-and-line, (**B**) gillnet, and (**C**) spear gun gear used at the three fishing grounds at Apo Island. Seasons: SW=southwest monsoon, INT=calm interim period, NE=northeast monsoon. Species groups: RA=reef associated species, RP=reef planktivores, RS=reef species, OW=open water species, OR=off-reef species. Percentages of dominant species groups are indicated. Legend for graphs at the left-hand side is at the upper right-hand side.

the western fishing grounds averaged 172 ±62 person hours/month. The total gillnet yield from this area was 493 kg (Table 1), dominated by reef species (64%, mainly Scaridae). Gillnet effort near Apo Reserve was much lower compared to other fishing grounds, averaging 78 ±27 person hours/month only. However, gillnet effort was relatively high near the reserve in July, October, and November (193, 155, and 157 person hours/month, respectively) (Fig. 2B). The total gillnet yield near the reserve was 318 kg (Table 1), dominated by reef species (63%, mainly Scaridae).

Gillnet effort did not differ significantly with seasons (ANOVA, $F_{1,18}$=0.18, P=0.68), but differed significantly among fishing grounds (ANOVA, $F_{2,18}$=6.72, P=0.007). The season by fishing ground interaction was significant (ANOVA, $F_{2,18}$=7.66, P=0.004). During the SW monsoon or interim period (July to October), gillnet effort on the northern fishing grounds was significantly higher than on the western fishing grounds (Tukey's test, $q_{3,18}$=5.68, P<0.005) and on the fishing grounds near Apo Reserve (Tukey's test, $q_{3,18}$=4.81, P<0.01) but did not differ between the latter two fishing grounds. During the NE monsoon (November to February), gillnet effort did not differ between the western and northern fishing grounds, but gillnet effort on the western fishing grounds was significantly higher than near Apo Reserve ($q_{3,18}$=4.47, P<0.025). Gillnet effort on the northern fishing grounds was higher during the SW monsoon and interim period than during the NE monsoon (Tukey's test, $q_{2,18}$=2.96, P=~0.05 [$q_{0.05,\ 2,18}$=2.97]). Conversely, gillnet effort on the western fishing grounds was significantly higher during the NE monsoon than during the SW monsoon and interim period (Tukey's test, $q_{2,18}$= 4.67, P<0.005). Gillnet effort near Apo Reserve did not differ significantly between seasons.

Spear gun fishing Spear fishing occurred mainly on the northern fishing grounds (Fig. 2C). However, spear

Table 1

Summary of recorded fishing effort, yield, and income of the fishery at Apo Island from 22 July 2003 to 29 February 2004. Contributions of the three fishing grounds (see Fig. 1) are shown. PHP = Philippine peso.

	Hook and line	Gill net	Spear gun	Fish trap	Overall
Total fishing effort (person hours)	8840	4141	452	129[1]	13,443[2]
Percent contribution					
Northern Apo Island	91.9	51.8	63.3	100	78.6
Western Apo Island	5.0	33.1	8.4	0	13.8
Near Apo Reserve	3.1	15.1	28.3	0	7.6
Total yield (kg)	3917	1535	406	32[3]	5890[3]
Percent contribution					
Northern Apo Island	90.6	47.2	66.2	100	77.7
Western Apo Island	5.2	32.1	4.8	0	12.1
Near Apo Reserve	4.2	20.7	29.0	0	10.2
Total income (PHP)	242,026	68,028	23,509	1371[3]	334,934[3]
Percent contribution					
Northern Apo Island	90.4	49.7	67.6	100	80.6
Western Apo Island	5.5	31.6	4.2	0	10.7
Near Apo Reserve	4.1	18.7	28.2	0	8.7

[1] Fishing effort in trap days = number of traps × number of days traps were left on the reef.
[2] Excludes fish trap effort.
[3] Trap yield in July not adjusted to 30-day period.

gun effort in this area declined from August to February (67 to 17 person hours/month, respectively). Spear gun effort on the northern fishing grounds averaged 36 ±6 person hours/month. The total spear gun yield from the northern fishing grounds was 269 kg (Table 1), dominated by reef-associated species (44%, Carangidae). Spear gun effort on the western fishing grounds was much lower, averaging only 5 ±3 person hours/month. It was highest in November (23 person hours/month) (Fig. 2C). The total spear gun yield from the western fishing grounds was only 19 kg (Table 1), dominated by reef species (62%, mainly Scaridae and octopus). Spear gun effort near the boundary of Apo Reserve was also rather low but was higher on average than on the western fishing grounds (mean 15 ±5 person hours/month). It peaked in October (44 person hours/month) (Fig. 2C). The total recorded spear gun yield near the reserve was 118 kg (Table 1), dominated by reef species (56%, mainly Scaridae and octopus).

Spear gun effort did not differ significantly between seasons (ANOVA, $F_{1,18}$=2.12, P=0.16) but differed significantly among fishing grounds (ANOVA, $F_{2,18}$=14.26, P<0.001). The season by fishing ground interaction was not significant (ANOVA, $F_{2,18}$=1.77, P=0.20). Spear gun effort on the northern fishing grounds was significantly higher than on the western fishing grounds (Tukey's test, $q_{3,18}$=7.41, P< 0.001) and the fishing grounds near Apo Reserve (Tukey's test, $q_{3,18}$=4.96, P<0.01). Spear gun effort, however, did not differ significantly between the fishing grounds near Apo Reserve and the western fishing grounds of Apo Island.

Trap fishing Bamboo fish traps were used on the northern fishing grounds only, and only in July (SW monsoon). The total trap effort was 126 trap days (4 fish traps set for 14 days, 7 for 10 days) with a total yield of 32 kg (Table 1). The yield was dominated by reef planktivores (85% Acanthuridae and Caesionidae).

Contributions of fishing gears and fishing grounds to overall fishing effort, yield, and income

Among the three principal fishing gear, most fishing effort was spent with hook and line, followed by gill nets, then with spear guns (Table 1). Hook-and-line fishing, therefore, contributed the greatest yield and highest income, accounting for 66% of the total yield and 72% of the total income recorded. Bamboo fish traps contributed the least yield and income (Table 1). All types of fishing occurred mainly on the northern fishing grounds. The northern fishing grounds accounted for 92%, 52%, 63%, and 100% of the total effort for hook-and-line gear, gill nets, spear guns, and fish traps, respectively. Accordingly, the northern fishing grounds accounted for the vast majority of total yield and total income for all types of fishing gears (Table 1).

On the other hand, fishing effort was often lowest on the fishing grounds near Apo Reserve (Table 1). The fishing grounds near the reserve accounted for only 3% and 15% of the total effort spent on hook-and-line and gillnet fishing, respectively. These fishing grounds contributed only 4% to the total yield and total income from hook and line fishing, and only 21% to the total

yield and 19% to the total income from gillnet fishing. Only 28% of the total spear gun effort was made near Apo Reserve. However, the overall spear gun effort near the reserve was about three times higher than that on the western fishing grounds. The fishing grounds near the reserve contributed about six times the yield and seven times the income of spear fishing on the western fishing grounds (Table 1).

Among species groups, the highest yield recorded was for reef-associated species, followed by reef planktivores, and then reef species (Table 2). Open water and off-reef species were minor contributors to overall yield. Reef-associated species together with reef planktivores accounted for 69% of the overall yield. The northern fishing grounds contributed ≥80% of the total yield of reef-associated species, reef planktivores, and open water species (Table 2). Much of the total yield of reef species (47%) was also taken from the northern fishing grounds. The western fishing grounds contributed 68% of the total yield of off-reef species but accounted for little of the yield for other species groups (Table 2). The fishing grounds near Apo Reserve often accounted for the smallest contribution to yield for all species groups. However, about a quarter of the total recorded yield of reef species were taken near the reserve.

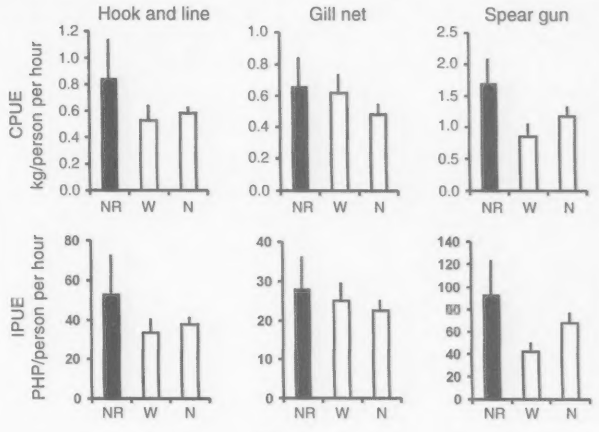

Figure 3

Mean catch per unit of effort (CPUE) and income per unit of effort (IPUE) for hook-and-line, gillnet and spear at the three fishing grounds at Apo Island. NR=near Apo Reserve, W=western Apo Island, N=northern Apo Island (see Fig. 1). Error bars are 1 standard error. PHP=Philippine peso.

Table 2

Composition of total recorded yield of the fishery at Apo Island from 22 July 2003 to 29 February 2004. Contributions of the three fishing grounds (see Fig. 1) are shown. Species groups: RA=reef-associated species, RP=reef planktivores, RS=reef species, OW=open water species, OR=off-reef species. Yield in July adjusted to 30-day period for each species group. Table excludes 16 kg of unidentifiable catch.

	RA	RP	RS	OW	OR
Total yield (kg)	2333	1772	1305	418	111
Percent contribution					
Northern Apo Island	92.4	85.6	46.7	80.0	7.9
Western Apo Island	3.9	9.1	28.4	3.6	67.5
Near Apo Reserve	3.7	5.2	24.9	16.4	24.6

Spatial patterns of CPUE and IPUE among fishing grounds

Mean hook-and-line, gillnet, and spear gun CPUE were highest in the fishing grounds near Apo Reserve (Fig. 3). CPUE near the reserve was higher than on the northern fishing grounds by a factor of 1.5, 1.4 and 1.4 for hook-and-line, gillnet, and spear fishing, respectively. CPUE near the reserve was higher than on the western fishing grounds by a factor of 1.6, 1.1 and 2.0 for hook-and-line, gillnet, and spear fishing, respectively. However, ANOVA indicated that CPUE (log [x+1] transformed) did not differ significantly among the three groups of fishing grounds ($F_{2,57}$=1.87, P=0.16), but differed significantly among fishing gear ($F_{2,57}$=9.26, P<0.001).

The trends in mean IPUE reflected closely those of CPUE (Fig. 3). Mean IPUE near the reserve was higher than on the northern fishing grounds by a factor of 1.4, 1.2, and 1.4 for hook-and-line, gillnet and spear fishing, respectively. It was higher than on the western fishing grounds by a factor of 1.6, 1.1 and 2.2 for hook-and-line, gillnet, and spear fishing, respectively. However, ANOVA indicated that IPUE (log [x+1] transformed) did not differ significantly among the three groups of fishing grounds ($F_{2,57}$=0.49, P=0.62), but differed significantly among fishing gear ($F_{2,57}$=6.77, P=0.002).

Monthly mean hook-and-line, gillnet, and spear gun CPUE and IPUE near Apo Reserve were more variable than in the other fishing grounds (Fig. 4, A–C). For example, the monthly hook-and-line CPUE near Apo Reserve changed from >1.5 to <1.0 to >2.0 and to <1.5 kg/person per hour from July to October. However, from November to February, it remained at <0.5 kg/person per hour, but was zero in January (Fig. 4A). Monthly hook-and-line IPUE near Apo Reserve varied accordingly. It changed from >100 to <50 to >150 and to <100 PHP/person per hour from July to October, but was less than 30 PHP/person per hour from November to February and was zero in January. In contrast, the monthly

hook- and-line CPUE and IPUE on the northern and western fishing grounds of Apo Island exhibited little variability (Fig. 4A). For most of the period between July and February, the monthly hook-and-line CPUE on the northern fishing grounds remained between 0.5 to 0.8 kg/person per hour, whereas IPUE remained between 30 to 50 PHP/person per hour. Monthly CPUE for the western fishing grounds remained mostly between 0.2 to 1.0 kg/person per hour, whereas monthly IPUE remained mostly between 15 to 60 PHP/person per hour.

Table 3

Range of monthly mean catch per unit of effort (CPUE) and income per unit of effort (IPUE) for hook-and-line, gillnet, and spear gun gear at the fishing grounds at Apo Island (see Fig. 1). Lowest minimum and highest maximum average values are marked by the symbol †. Highest minimum values are marked by ‡. PHP = Philippine peso.

	Hook and line	Gill net	Spear gun
CPUE (kg/person per hour)			
Northern Apo Island	0.3‡–0.8	0.2‡–0.7	0.7‡–2.0
Western Apo Island	0.1–1.0	0.2‡–1.3	0.2†–1.5
Near Apo Reserve	0.0†–2.4†	0.1†–1.6†	0.5–3.9†
IPUE (PHP/person per hour)			
Northern Apo Island	18.4‡–49.00	9.6‡–31.30	40.30‡–117.60
Western Apo Island	6.20–58.40	8.20–46.40	11.90†–57.80
Near Apo Reserve	0†–154.90†	7.80†–73.70†	30.50–249.90†

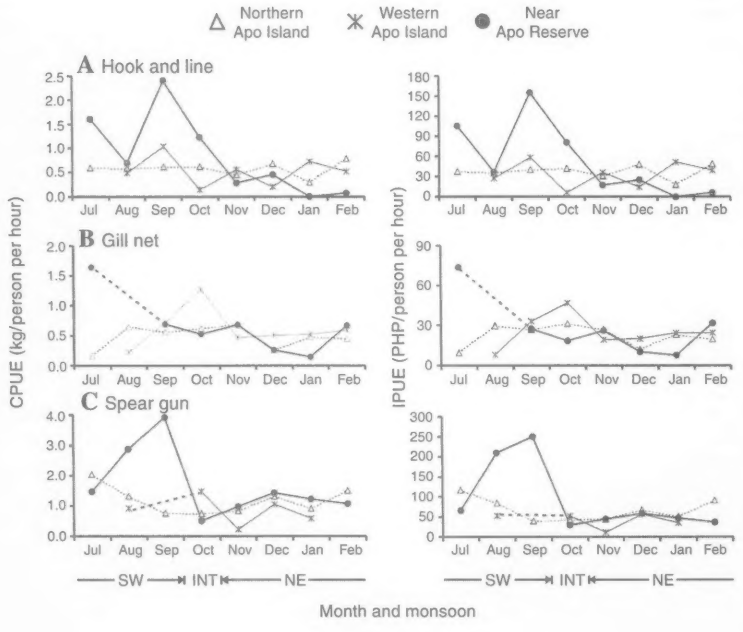

Figure 4

Monthly mean catch per unit of effort (CPUE) and income per unit of effort (IPUE) for (**A**) hook-and-line, (**B**) gill-net, and (**C**) spear at the three fishing grounds at Apo Island. Seasons: SW=southwest monsoon, INT=calm interim period, NE=northeast monsoon. PHP=Philippine peso.

Fishing grounds near Apo Reserve often had the lowest minimum monthly CPUE and IPUE for all fishing gears, except for spear gun, which had the lowest minimum monthly CPUE and IPUE on the western fishing grounds (Table 3). However, fishing grounds near Apo Reserve always had the highest maximum monthly CPUE and IPUE for all fishing gears (Table 3, Fig. 5). Maximum monthly CPUE near the reserve was higher by a factor of 1.2 to 3.0, depending on the fishing gear and fishing ground (Fig. 5). Maximum monthly IPUE near the reserve was higher by a factor of 1.6 to 4.3, depending on the fishing gear and fishing ground. On the other hand, the highest minimum monthly CPUE and IPUE for all fishing gears were most often found only on the northern fishing grounds of Apo Island (Table 3).

Spatial patterns of high-value catches among fishing grounds

Capturing high-value species and landing a high yield of such species were often more frequent on the northern fishing grounds (Table 4). For example, 133 captures of high-value reef-associated species (Carangidae—*Caranx ignobilis* (Forsskål), *Caranx melampygus* (Cuvier), and *Carangoides* sp.) were made on the northern fishing grounds. In 46 of these captures, the yield was ≥7.0 kg or 525 PHP. Six of the fishes cap-

Table 4

Frequency and probability of capturing or landing a high yield of high-value species within each species group for each of the three fishing grounds at Apo Island (see Fig. 1). Upper values: frequency (number of fishing trips) and probability (in parentheses) of capturing high-value species. Lower values: frequency (number of fishing trips) and probability (in parentheses) of landing a high yield of high-value species. Highest frequencies are marked with the symbol †. Highest probabilities are marked with the symbol ‡. Price per kg and prices of what were considered "high yield" are given in Philippine pesos (PHP).

Species groups, families	Northern Apo Island	Western Apo Island	Near Apo Reserve
Reef-associated species (Carangidae)			
75 PHP/kg	133† (0.07)‡	9 (0.03)	8 (0.05)
≥7.0 kg or PHP 525	46† (0.03)‡	1 (0.004)	4 (0.02)
Reef planktivores (Caesionidae)			
55 PHP/kg	123† (0.07)‡	17 (0.06)	9 (0.05)
≥3.0 kg or PHP 165	36† (0.03)‡	4 (0.02)	0 (0)
Reef species (Serranidae, Lutjanidae, Lethrinidae)			
70–75 PHP/kg	57† (0.03)	15 (0.06)	12 (0.07)‡
≥2.0 kg or PHP 150	31† (0.02)	10 (0.04)	9 (0.05)‡
Open water species (Scombridae)			
75–90 PHP/kg	5† (0.003)	1 (0.01)‡	0 (0)
≥7.0 kg or PHP 525	3† (0.002)‡	0 (0)	0 (0)
Off-reef species (Lutjanidae)			
75 PHP/kg	4 (0.003)	29† (0.23)‡	3 (0.04)
≥2.0 kg or PHP 150	2 (0.001)	13† (0.10)‡	2 (0.03)

tured weighed ≥15 kg (equivalent to a value of ≥1125 PHP). The largest was a 31.9-kg *C. ignobilis* valued at 2393 PHP, which was also the biggest fish caught during our study. In contrast, only eight captures of high-value reef-associated species were made near Apo Reserve. In only four of these captures were the yields ≥7.0 kg or 525 PHP. Only one of the fishes captured near the reserve weighed >15 kg. This was a 20.2-kg *C. ignobilis* valued at 1515 PHP.

Capturing high-value species and landing a high yield of such species often had the greatest probability of occurring on the northern fishing grounds (Table 4). For example, the probability of capturing high-value reef-associated species from the northern fishing grounds was 0.07. Landing a high yield of such species from this area had a probability of 0.03. In contrast, the probability of capturing high-value reef-associated species near Apo Reserve was 0.05. Landing a high yield of such species near the reserve had a probability of 0.02. However, the probability of capturing high-value reef species (Serranidae—*Cephalopholis*, *Epinephelus*, *Variola* spp.; Lutjanidae—*Aprion*, *Lutjanus*, *Macolor*, *Symphorichthys*, *Symphorus* spp.; and Lethrinidae—*Lethrinus* spp.) was greatest near Apo Reserve (Table 4). The probability of landing a high yield of such species (≥2.0 kg or 150 PHP) was also greatest near the reserve, despite the higher frequency of capturing high-value reef species, or landing a high yield of such species, on the northern fishing grounds than near Apo Reserve (Table 4).

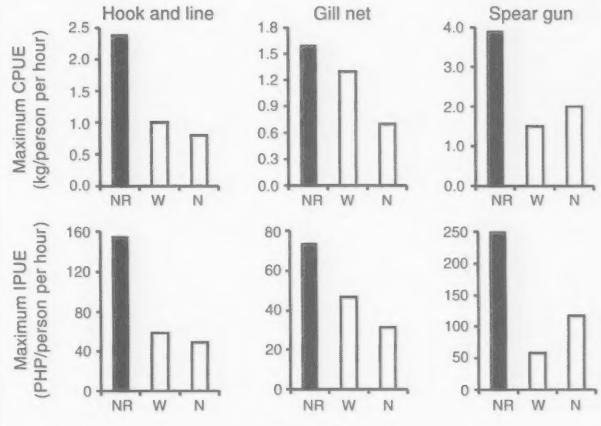

Figure 5

Maximum monthly mean catch per unit of effort (CPUE) and income per unit of effort (IPUE) for hook-and-line, gill-net, and spear gun gear used at the three fishing grounds at Apo Island. NR=near Apo Reserve, W=western Apo Island, N=northern Apo Island (see Fig. 1). Error bars are 1 standard error. PHP=Philippine peso.

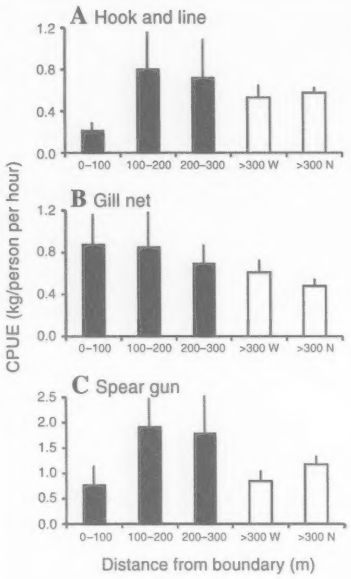

Figure 6

Mean catch per unit of effort (CPUE) for (**A**) hook-and-line, (**B**) gillnet, and (**C**) spear gun gear deployed at three distances from the boundary of Apo Reserve (0–100, 100–200, 200–300 m [shaded columns]; refer to Fig. 1) and at two areas far (>300 m) from reserve boundaries (W=western Apo Island fishing ground, N=northern Apo Island fishing ground [open columns]; refer to Fig. 1). Error bars are 1 standard error.

Spatial patterns of CPUE near reserve boundaries

Spatial patterns of CPUE away from reserve boundaries differed for hook-and-line, gillnet, and spear gun gear (Fig. 6). Gillnet CPUE exhibited a pattern of decrease from 0–100 to 200–300 m from the reserve boundaries (from 0.88 to 0.70 kg/person per hour; Fig. 6B). Gillnet CPUE further decreased >300 m from reserve boundaries (western and northern fishing grounds). In contrast, hook-and-line and spear gun CPUE was lowest near (0–100 m) reserve boundaries, but much higher at distances of 100–300 m from the boundaries (Fig. 6, A and C). Hook-and-line and spear gun CPUEs at 100–300 m from reserve boundaries were higher than farther away (>300 m) from the boundaries (western and northern fishing grounds). However, hook-and-line and spear gun CPUEs were highest at 100–200 m from reserve boundaries (Fig. 6, A and C). An ANOVA with data for 0–300 m indicated only that CPUE did not differ significantly with distance from reserve boundaries ($F_{2,39}$=0.73, P=0.49) or with fishing gear ($F_{2,39}$=2.52, P=0.09). However, an ANOVA with data for 0–300 and >300 m indicated that CPUE (log [x+1] transformed) did not differ significantly with distance from reserve boundaries ($F_{4,76}$=1.19, P=0.32) but differed significantly among fishing gear ($F_{2,76}$=7.28, P=0.001).

Table 5

Frequency of fishing trips for each of the three distances from the boundaries of Apo Reserve (see Fig. 1), for each of hook and line, gill net, and spear gun. Fishing trips were made between 22 July 2003 and 29 February 2004.

	Number of times fished		
	Hook and line	Gill net	Spear gun
Distance from reserve boundaries			
0–100 m	2	3	4
100–200 m	43	24	33
200–300 m	25	28	7

Contrasting patterns were also found in fishing effort (frequency of fishing trips) at different distances from the boundaries of Apo Reserve (Table 5). Hook-and-line and spear fishing occurred most frequently at intermediate distances from reserve boundaries, but gillnet fishing occurred most frequently at the farthest distances. However, all types of fishing occurred very infrequently within 100 m of reserve boundaries (Table 5).

Discussion

Results indicate that the maximum possible contribution of spillover from the no-take reserve to the overall yield and income of the fishery at Apo Island is small. If one assumes that the spillover of coral reef fishes is most likely to operate on spatial scales of hundreds of meters (Russ, 2002), and, thus, would be unlikely to affect fishery yields on the western and northern fishing grounds, the maximum possible contribution would be 10% of the total fishery yield, but the real value is probably much less than this. We assumed that the eight months sampled in 2003–2004 are representative of the general spatial pattern of fishing at Apo Island. Furthermore, we assumed that the spatial pattern of fishing during the four months not sampled (March to June) remains consistent with the general pattern of fishing. It can be estimated from the present study that the total fishery yield at Apo Island in 2003–2004, excluding the yield consumed locally, was around 10.4 tons/km^2 per year (to the 60-m isobath). Thus, spillover from Apo Reserve would have contributed very much less than 1.0 ton/km^2 per year in 2003–2004.

Fishing effort was often lowest on the fishing grounds near the reserve. The fishery at Apo Island is primarily hook and line, targeting reef-associated species (Carangidae), and to a lesser extent reef planktivores (*Naso*

spp.) (Alcala and Luchavez, 1981; White and Savina, 1987; Bellwood, 1988; Maypa et al., 2002; present study). Ninety-two percent of total hook-and-line effort was made on the northern fishing grounds of the island. Gill nets, spear guns, and fish traps were not used as much as hook-and-line; however, fishing with these gear was also carried out mostly on the northern fishing grounds, contributing to a yield of reef-associated species and reef planktivores. Fishing near Apo Reserve contributed mainly to catch of reef species (Scaridae and octopus), which are a less important species group for the local fishery. The fishery depended heavily on access to the northern fishing grounds during the SW monsoon and calm interim period (Bellwood, 1988; present study). Results clearly showed that fishing effort on the northern fishing grounds was considerably lower during the NE monsoon, especially for hook-and-line gear and gill nets. However, fishing effort did not shift to the fishing grounds near Apo Reserve during the NE monsoon. Gillnet fishing seemed to transfer instead to the western fishing grounds, targeting reef species (Scaridae). To a much lesser degree, hook-and-line fishing also transferred to the western fishing grounds, targeting high-value off-reef species (*Aphareus furca* [Lutjanidae]). The northern fishing grounds alone accounted for 78% of overall yield and 81% of overall income recorded in our study (Table 1). In contrast, fishing grounds near Apo Reserve accounted for only 10% of overall yield and 9% of overall income (Table 1). However, it is highly unlikely that spillover from Apo Reserve supplied the entire yield taken from fishing grounds near the reserve. That is, the yield near the reserve was probably not composed totally of migrants from the reserve. Therefore, the actual spillover contribution of Apo Reserve would be much less than 10% to the overall yield and income generated by the fishery.

However, CPUE of fishermen was highest on the fishing grounds near Apo Reserve. This pattern may have resulted from 1) spillover from the reserve or 2) lower fishing intensity near the reserve, resulting in higher abundance of fish and, thus, higher CPUE. There is far more empirical evidence supporting the spillover hypothesis than the lower fishing intensity hypothesis. Considerable evidence exists that some supplement for the fishery near the reserve has developed over time. Firstly, monitoring of Apo Reserve since 1983 has shown that fish populations inside the reserve have increased in abundance, some having tripled in density or biomass over the last two decades (Russ and Alcala, 1996, 1998, 2003; Russ et al., 2003, 2004; Alcala et al., 2005). Secondly, long-term monitoring indicates that the reserve began to export adult fish to a site open to fishing after ~8 years of reserve protection (Russ and Alcala, 1996; Russ et al., 2003, 2004). Thirdly, catch rates of some species (Acanthuridae) were found to be higher near the reserve than elsewhere around Apo Island after two decades of reserve protection (Russ et al., 2003, 2004). Fourthly, recent studies indicate that patterns of decreasing abundance of some targeted species are present across the northern boundary of the reserve (Abesamis et al., 2005). Lastly, a recent study indicates that density-dependence may be driving net emigration of adult fish (*Naso vlamingii* (Valenciennes)) from the reserve (Abesamis and Russ, 2005). On the other hand, no direct evidence is available to show that fishing effort near Apo Reserve has remained low over the last two decades. However, the fishing grounds near the reserve may be partially exposed to the SW and NE monsoons (Alcala and Luchavez, 1981). During the SW monsoon, the fishing grounds adjacent to the southern end of the reserve may become rough, but those adjacent to the northern end are usually calm (Fig. 1). The pattern is reversed during the NE monsoon. Thus, fishing effort near the reserve may be reduced for nine months of the year (June to September, November to March) because only the area close to one side of the reserve may be fished, depending on the monsoon. The role of the monsoons in limiting fishing effort near the reserve cannot be ruled out entirely.

If spillover has increased CPUE near the reserve, as long-term evidence seems to indicate, then why have local fishermen not responded noticeably to the improvement in catch rates? Weather may be important in limiting fishing effort near the reserve, but it cannot explain the low fishing intensity in this area during the calm interim months. Results show that hook-and-line and gillnet effort on the fishing grounds near the reserve in October were still considerably lower than on the northern fishing grounds (Fig. 2, A and B). Anecdotal information also indicates that most fishermen still prefer to fish the northern fishing grounds even during April and May (Pascobello[2]). This information is consistent with the findings of previous studies (White and Savina, 1987; Bellwood, 1988; Maypa et al., 2002), which indicate that the general pattern of fishing effort at Apo Island has not changed much since creation of the reserve in 1982. Furthermore, a reasonable amount of fishing area (8–11 ha) near the reserve is still available to fishermen during either monsoon. Given the higher catch rates, fishermen could still concentrate effort near the reserve, one side of the reserve at a time, depending on the monsoon. Higher costs (time and energy spent to paddle a small boat [*banca*]) are certainly not preventing fishermen from fishing adjacent to the reserve. The majority of fishermen (80%) reside near the reserve, in Baybay and Ubos villages (Fig. 1) and therefore for most fishermen the costs of fishing the northern side of Apo Island may actually be higher. It is also unlikely that fishermen are not aware of higher catch rates near the reserve. Fishermen can probably obtain good information about catch rates from the experiences of fellow fishermen, or from word-of-mouth, because the community is relatively small and tightly knit. Many fishermen are members of the same family (including cousins and uncles) or are friends with each other. Income rates *per se* can also be ruled out as an

[2] Pascobello, M. 2002. Personal commun. Apo Island resident and village chairman. Apo Island, Dauin Municipality, Negros Oriental, Philippines, 6217.

important influence on the spatial pattern of effort because results indicated that IPUE for all gears was also highest on the fishing grounds near the reserve. However, one cannot discount that the northern side of Apo Island may be regarded by the local community as their main traditional fishing ground. This area has probably been fished for decades, providing the income for families generation after generation.

Other characteristics of the CPUE and IPUE data may also provide a partial explanation. CPUE and IPUE were more variable on the fishing grounds near Apo Reserve (Fig. 4). In fact, the fishing grounds near the reserve often had both the highest and lowest CPUE and IPUE per month for all types of fishing gears (Table 3, Fig. 5). The only exception was for spear gun, which had the lowest CPUE and IPUE on the western fishing grounds (Table 3). These findings may indicate that near the reserve, fishermen could obtain very high average monthly catch rates and income rates. However, they may also indicate that near the reserve, fishermen (using hooks and lines and gill nets) could obtain very low average monthly catch rates and income rates. Monthly CPUE and IPUE were least variable on the northern fishing grounds (Fig. 4). In addition, the highest minimum average monthly CPUE and IPUE were always found in this area (Table 3). Therefore, a plausible explanation for the spatial pattern of fishing effort at the island scale is that fishermen probably tend to avoid fishing near Apo Reserve in order to make their monthly incomes more stable and avoid occasional very low catch rates. Fishermen may prefer the northern fishing grounds even if catch rates in this area are not as high as near the reserve because they are assured of obtaining higher minimum yields and a more stable income. This strategy may be a form of financial "risk aversion" (Hilborn and Walters, 1992). It is further postulated that such a risk aversion strategy could explain why total spear gun effort was higher on the fishing grounds near Apo Reserve than on the western fishing grounds (Tables 1 and 3). Also, a risk aversion strategy may partly explain why fishing with gill nets and hook and line transferred to the western fishing grounds instead of near the reserve during the NE monsoon (Fig. 2B, Table 3).

Other factors may also influence the decision by fishermen to concentrate effort on the northern side of Apo Island. For example, the largest and most valuable fish recorded in this study, a 31.9-kg *Caranx ignobilis* worth almost PHP 2400, was captured from the northern fishing grounds. A high-priced catch such as this one may have a tremendous psychological impact on local fishermen. Anecdotal information seems to indicate that the income from such a yield may be enough to provide for 80% of the daily expenses of one family for one month at Apo Island (Pascobello-Rhodes[3]). In comparison, the largest and most valuable fish caught near Apo Reserve, also *C. ignobilis*, was only two-thirds the weight (20.2 kg) and value (PHP 1515) of the largest fish caught from the northern fishing grounds. This fish was the only one caught near the reserve with a value greater than PHP 1000. Local fishermen probably consider fish of this size more common on the northern fishing grounds. During this study, five individuals of *C. ignobilis* (range: 15.0–19.0 kg) that were captured from the northern fishing grounds had weights similar to the largest fish caught near the reserve. Therefore, the biggest psychological impact on fishermen may not be due to spillover from the reserve.

A perception by local fishermen that the northern fishing grounds are productive areas for high-value species may not only have a psychological basis. Results indicate that the probability of capturing high-value reef-associated species (Carangidae) and the probability of landing a high yield of such species were highest on the northern fishing grounds (Table 4). The same was true for high-value reef planktivores (Caesionidae) (Table 4). The probability of landing a high yield of high-value open water species (Scombridae) was also greatest on the northern fishing grounds (Table 4). Assuming that fishermen prefer to target high-value species, these findings indicate that fishermen have better chances of making higher incomes from the northern fishing grounds than from other areas. The better prospect of making a higher income probably influences the decision by fishermen to concentrate effort on the northern side of Apo Island whenever it is accessible. Similarly, some fishermen probably shift to the western fishing grounds during the NE monsoon (the "off-season") because of better chances of gaining higher incomes by targeting high-value off-reef species (*A. furca* [Lutjanidae]) (Table 4).

However, the results indicated that the probability of capturing high-value reef species (Serranidae, Lutjanidae, and Lethrinidae), or landing a high yield of such species, was greatest on the fishing grounds near Apo Reserve (Table 4). Fishing intensity for high-value reef species, on the other hand, appears to be greatest on the northern fishing grounds, because capturing or landing a high yield of high-value reef species was most frequent there (Table 4). Thus, it seemed that most fishermen avoided fishing for high-value reef species near Apo Reserve despite better chances of making high incomes from high-value reef species. One plausible explanation for avoiding the fishing grounds hear the reserve is that fishermen would still prefer to fish the northern fishing grounds because they can target the high-value species that come in larger sizes (Carangidae and Scombridae) or greater numbers (Caesionidae) and at the same time occasionally capture high-value reef-species. The high-value reef species (Serranidae, Lutjanidae, Lethrinidae) are unsatisfactory alternatives for fishermen because they come in smaller sizes (compared to Carangidae and Scombridae) or in smaller numbers (compared to Caesionidae), and therefore would fetch a lower price.

[3] Pascobello-Rhodes, L. 2003. Personal commun. Apo Island resident. Apo Island, Dauin Municipality, Negros Oriental, Philippines, 6217.

On the other hand, the highest maximum monthly CPUE and IPUE were invariably found near Apo Reserve (Fig. 5, Table 3). This result is consistent with the occasional spillover of bigger fish from the reserve. Such an effect may have a positive influence on the attitudes of fishermen toward reserves (Russ and Alcala, 1996). However, in the case of the artisanal fishery at Apo Island, any psychological impact of large catches near the reserve on fishermen is probably attenuated by the importance of the northern fishing grounds. In other fisheries, however, occasional spillover of large adults may be important. Recreational "trophy" fisheries, for example, may benefit directly from such an effect of no-take reserves (Bohnsack, 1998; Johnson et al., 1999; Roberts et al., 2001). In New Zealand, Kelly et al. (2002) showed that lobster catch rates (kg/trap haul) were similar close to and far from Leigh Marine Reserve, although catches around the reserve consisted of fewer individuals. The lobsters caught near the reserve were bigger. Furthermore, the amount of money made per trap haul close to the reserve was similar to sites far from the reserve.

The findings at the scale of a few hundred meters from the boundary of the reserve provide little evidence to indicate that spillover from Apo Reserve is present. In fact, the most informative result at this spatial scale was that fishermen seemed to avoid fishing very close to the reserve (i.e., within 100 m from the boundaries) (Table 5). Furthermore, catch rates seemed to be lowest closest to reserve boundaries for hook-and-line and spear fishing (Fig. 6, A and C). However, gillnet fishing seemed to have a pattern of decreasing catch rate away from reserve boundaries (Fig. 6B). Gear selectivity interacting with the spatial distribution of target species may explain the differences in spatial patterns of CPUE among the three gears. Gillnet fishing is probably less selective than hook-and-line and spear fishing.

The pattern of fishing effort found very near to the reserve can be interpreted in two ways. Firstly, local fishermen may be well aware of the distribution of catch rates near Apo Reserve, and they adjust their fishing effort accordingly. This interpretation is supported to some degree by the correspondence between the pattern of CPUE and the pattern of fishing effort for hook-and-line and spear gun gear. Both CPUE and fishing effort for these gear were highest at intermediate distances (100–200 m), but lower at the closest (0–100 m) and farthest distances (200–300 m) from the reserve (Fig. 6, A and C, Table 5). Fishermen may know from experience that hook-and-line and spear gun catch rates are low nearest the reserve (0–100 m), hence they tend to avoid fishing in this area. Experimental fishing with hooks and line, but specifically targeting *N. vlamingii*, supports the contention that hook-and-line CPUE is low very close to the boundary of Apo Reserve (Abesamis and Russ, 2005). Hook-and-line CPUE for *N. vlamingii* was higher at intermediate distances (150–200 m) than at the closest (50–100 m) and farthest (250–300 m) distances from the reserve (Abesamis and Russ, 2005). Although movement of fish from Apo Reserve to sites at intermediate distances (100–200 m) from the reserve has never been demonstrated directly, research in the last two decades has shown that fish populations (Acanthuridae, Carangidae, Serranidae, Lutjanidae, and Lethrinidae) have increased outside but close to the southern boundary of the reserve (about 200–250 m from that boundary) after about eight years of reserve protection (Russ and Alcala, 1996; Russ et al. 2003, 2004). This increase in populations may indicate that the present spatial distribution of hook-and-line and spear gun effort at the local scale may reflect the response of a small number of fishermen to spillover from the reserve.

Secondly, local fishermen may avoid fishing very close to the boundaries of Apo Reserve in order to prevent being accused of poaching inside the reserve. The inconsistent result of a higher catch rate but lower fishing effort nearest the reserve for gillnet fishing supports this idea (Fig. 6B, Table 5). Furthermore, there may be tremendous motivation for resident fishermen not to be implicated in poaching inside the reserve. The ultimate reason for this probably lies in the smallness of the community at Apo Island. Almost everyone has known each other for most of their lives. The no-take reserve was established by the community for their own benefit (Russ and Alcala, 1999). It has been guarded and maintained by community members, many of them fishermen themselves, for most of the two decades of its existence (Russ and Alcala, 1999). It has an important role in tourism on the island, from which the local community has benefited considerably in many ways (Alcala, 1998; Russ and Alcala, 1999). It is the principal factor that has made Apo Island a nationally and internationally recognised model for successful, community-based resource management (Alcala, 1998; Russ and Alcala 1999). Many residents are probably aware of most, if not all, of these achievements. For these reasons, it is clearly against the best interests of a resident fisherman, and his family, to be labeled by fellow community members as a threat to the security of their reserve.

In conclusion, this study has shown that spillover yield from the no-take reserve at Apo Island probably contributes much less than 10% of the overall yield to the local fishery. Fishing effort was often lowest near the reserve, despite higher catch rates there. The finding of low fishing intensity near reserve boundaries despite indications of spillover contrasts with most empirical evidence collected so far (e.g., Gell and Roberts, 2003) and recent theoretical studies (e.g., Salomon et al., 2002) indicate that spillover will increase fishing effort near reserve boundaries. Fishing effort adjacent to the reserve appears to be limited by 1) weather determined by the monsoons, 2) the traditional importance of the northern fishing grounds, 3) high variability of catch rates and income rates, 4) lower value of target species found near the reserve, and 5) social pressures related to the history of community management of the reserve. However, the present study has no information on how fishing effort, yield, and catch rates near the reserve have changed over the past 20 years since

reserve establishment. Despite the Apo Island fishery being one of the best studied coral reef fisheries in the world (Alcala and Luchavez, 1981; White and Savina, 1987; Bellwood, 1988; Maypa et al., 2002; Russ et al, 2004; Alcala et al., 2005), the present study is the first to quantify detailed spatial variations in fishing effort, catch, and CPUE at Apo Island. Furthermore, it is not clear if spillover yield to the local fishery has reached its full potential or not. Long-term fishery monitoring is required to answer these questions. Although the reserve probably provides limited direct benefits to the local fishery through spillover, its indirect benefits to the community at Apo Island are considerable. The reserve became the foundation for a program of fishery conservation for the whole island, which eliminated unsustainable fishing practices such as dynamite fishing and muro-ami drive-net fishing. It played a critical role in enhancing tourism activities on the island, which had a tremendous positive effect on the standard of living of the local community (Russ and Alcala, 1999; White et al., 2002). These indirect effects of reserve establishment are arguably as important as the direct benefits of reserves to developing areas of the world. It remains to be seen whether successful reserves such as Apo Reserve have broader-scale direct benefits to fisheries through net larval export.

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Comparing the identification of southern California juvenile rockfishes (genus *Sebastes* spp.) by restriction site analysis of the mitochondrial ND3/ND4 region and by morphological characteristics

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Abstract—Rockfish (*Sebastes* spp.) juveniles are often difficult to identify by using morphological characters. This study independently applies morphological characters and a key based on mitochondrial restriction site variation to identify juvenile rockfishes collected in southern California during juvenile rockfish surveys. Twenty-four specimens of *Sebastes* were examined genetically without knowledge of the morphological assignment. Seventeen fish were identified genetically as *S. semicinctus*, *S. goodei*, *S. auriculatus*, *S. jordani*, *S. levis*, *S. rastrelliger*, and *S. saxicola*. Identities for the remaining fish were narrowed to two or three species: 1) three fish were either *S. carnatus* or *S. chrysomelas*; 2) one fish was either *S. chlorosticus*, *S. eos*, or *S. rosenblatti*; and 3) three fish could have been either *S. hopkinsi* or *S. ovalis*, the latter for which we now have distinguishing mitochondrial markers. The genetic and morphological assignments concurred except for the identity of one fish that could only be narrowed down to *S. hopkinsi* or *S. semicinctus* by using morphological characters. Genetics excluded more species from multispecies groupings than did the morphological approach, especially species within the subgenus *Sebastomus*. Species in the genetically unresolvable groups may be similar because of recent divergence or because of interspecies introgression.

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Sixty-five rockfish species (*Sebastes* spp.) inhabit the waters along the California coast (Moser, 1996). Within the genus, there is a high degree of similarity among many species in morphological characters. These similarities are in part due to recent divergence, but may also have resulted from convergence of congeners occupying similar habitats. Identification of *Sebastes* (and most species) is usually based on morphology; however, this approach may fail, especially for identifying sympatric species, which can be similar in coloration and overlap in morphological characters. Juvenile rockfishes are morphologically distinct from larvae and adults (Kendall, 2000), and juvenile stages of many species, especially the pelagic juvenile stage, have not yet been described; only a few species have complete ontogenetic descriptions (Matarese et al.,1989; Moser, 1996). The species of a few *Sebastes* larvae can be determined and adults can be misidentified.

Rockfishes are important ecologically and some species are economically valuable. *Sebastes* larvae are a large component of ichthyoplankton collections and rank third or fourth in abundance among all fish larvae taken during California Cooperative Fisheries Investigations (CalCOFI) surveys, which cover the entire length of the California and Baja California coast and now survey southern California. The ability to identify *Sebastes* accurately and efficiently at all developmental stages will, in turn, greatly increase our knowledge of their life histories, as well as our management and conservation efforts. An increased understanding of life history variation can improve the systematic descriptions of *Sebastes* species, which have mostly been based on the morphology of adults.

The analysis of restriction site variation of polymerase chain reaction (PCR)-amplified mtDNA is an effective and relatively simple method for species identification of adult specimens of fish species. The use of restriction enzymes to cleave the DNA can reveal variation in the mtDNA sequence at specific sites, and individuals or species can often be distinguished by the presence or absence of these sites. This method has advantages over sequencing in that it can be conducted relatively easily and used to survey large stretches of a DNA sequence, whereas sequencing,

because of its high cost, is usually limited to a much smaller span of DNA. Closely related species of several genera have been identified with this method; for example, snappers (Chow et al., 1993), eels (Aoyama et al., 2000; Lin et al., 2002), billfishes (Innes et al., 1998), and rockfishes (Gharrett et al., 2001). For identification of larvae and juveniles, restriction site patterns of adults can be used as references to ensure the reliability of the results. A limited database was used and a small number of samples were tested for a previous report on larval and juvenile identification of *Sebastes*, also based on restriction patterns of the mtDNA (Taylor, 1998).

The objective of this study was to compare the results of identifying pelagic juvenile rockfishes by the application of a key for delineating species based on mtDNA variation of adult rockfishes (Li et al., 2006) and by using only morphological characteristics. The questions we addressed were the following: Are the results for both genetic identifications and morphological identifications concordant? If not, how did these two methods differ? The targets of the comparison were samples of pelagic juvenile rockfishes collected from southern California. Both genetic and morphological analyses were conducted without knowledge of the results of the other.

Table 1

Sample identification numbers, sampling location, standard length (SL), weight, and method of tissue storage of juvenile specimens of *Sebastes* spp. Missing sample numbers are those for which the DNA could not be amplified: a = frozen on the boat, thawed on ice when genetic material was taken; b=put into ethanol on the boat.

Sample number	North latitude	West longitude	SL (mm)	Weight (g)	Preservation technique
1	34.20	120.24	41.3	1.200	a
2	"	"	42.2	1.282	a
3	"	"	35.8	0.756	a
4	"	"	36.1	0.777	a
5	"	"	31.0	0.478	a
8	"	"	29.5	0.360	a
9	"	"	24.1	0.206	a
15	34.26	120.15	28.9	0.265	b
16	"	"	37.6	0.565	b
17	"	"	34.0	0.654	b
18	"	"	23.2	0.150	b
19	"	"	26.0	0.326	b
20	"	"	35.1	0.591	b
21	"	"	24.8	0.273	b
22	"	"	22.6	0.190	b
23	"	"	21.0	0.140	b
25	"	"	25.0	0.273	b
26	34.23	119.93	27.6	0.472	b
27	"	"	26.8	0.235	b
31	"	"	28.0	0.345	b
44	"	"	37.9	0.799	b
45	"	"	35.6	0.590	b
48	"	"	24.2	0.189	b
49	"	"	24.3	0.168	b

Materials and methods

Collection of juveniles

Juvenile rockfishes were collected from the coast of Santa Barbara, California in June of 1998 and 2000 (Table 1). Fish were captured at night with a modified Cobb mid-water trawl with a nominal 12.2 m×12.2 m opening and 9-mm mesh net. Average trawling depth ranged from 18 to 29 m below the surface and above bottom depths ranged from 500 to 800 m, except for one specimen that was caught over a bottom depth of 88 m. Generally, specimens were sorted and then frozen on board the vessel. However, specimens from two hauls were sorted and immediately put in 95% ethanol aboard the vessel. Similar collection methods were used for both years. Details of the 1998 survey are provided in Nishimoto and Washburn (2002). The standard lengths (mm) of the specimens ranged from 16 to 42 mm.

Genetic identification

Following collection, each fish was identified in the laboratory by using morphological characters and meristics and pigmentation patterns. Specimens were chosen for genetic examination based on morphological differences. Fish representing different developmental stages (e.g., transition from larval to pelagic juvenile stage) of a species were included in the sample. We examined forty-nine specimens that included species that were easily identified based on pigmentation and morphological characters and individuals for which identification was less certain. All specimens were provided for genetic analysis without information on the morphological assignment.

For the genetic analysis, muscle tissue and skin from one side of the body was removed from each specimen in September 2000. Total genomic DNA was isolated by using a Purgene DNA™ isolation kit (Gentra Systems, Inc., Minneapolis, MN). Total DNA of each specimen was PCR-amplified and digested with specific restriction enzymes as directed in the key (Li et al., 2006). In some cases, digests with additional restriction enzymes were conducted to increase certainty of the identifications. Restriction fragments were separated electrophoretically on 1.5% agarose gels (one part agarose [Sigma-Aldrich, St. Louis, MO] and two parts Synergel™ [Diversified Biotech Inc., Boston, MA]) in 0.5×TBE buffer (TBE is 90 mM Tris-boric acid, and

Table 2

The most commonly occurring count (majority) and range of counts of dorsal-, anal-, and pectoral-fin rays among adults of *Sebastes* spp. identified in this study and for species that have morphologically similar pelagic juveniles or that are yet undescribed. (Compiled from Laidig and Adams, 1991; Moser, 1996; Love et al., 2002). Grouping of species is explained in the text.

	Dorsal-fin rays		Anal-fin rays		Pectoral-fin rays	
Species	Majority	Range	Majority	Range	Majority	Range
Species with distinct morphological characteristics						
S. levis	12–13	12–13	7	6–7	18	17–18
S. goodei	14	13–16	8	7–9	17	16–18
S. jordani	14–15	13–16	9–10	8–11	20–21	19–22
Group I						
S. saxicola	12	11–14	7	5–8	16	15–18
S. rastrelliger	13	12–14	6	6	19	18–20
S. semicinctus	13	12–14	7	6–8	17	16–18
S. auriculatus	13	12–15	7	5–8	18	15–19
S. wilsoni	13–14	13–15	6	5–7	17	16–18
S. hopkinsi	14–15	13–17	7	6–9	17	16–18
S. ovalis	14–16	13–16	8–9	7–9	18	17–19
Group II						
S. caurinus	12–13	11–14	6	5–7	17	16–18
S. carnatus	13	12–14	6	5–7	17	16–18
S. chrysomelas	13	12–14	6	5–7	17	17–18
S. atrovirens	14	12–15	7	6–8	17	16–18
Sebastomus group						
S. rosenblatti	12	11–13	6	5–6	17	16–18
S. lentiginosus	12	12–13	6	6–7	17	16–18
S. eos	12–13	11–13	6	5–7	17–18	16–18
S. umbrosus	12–13	11–14	6	5–7	16–17	15–18
S. rosaceus	12–13	11–14	6	5–7	17	16–18
S. chlorostictus	12–13	11–15	6	5–7	17	16–18
S. helvomaculatus	13	12–14	6	5–7	16–17	15–18
S. constellatus	13	12–14	6	5–7	17	16–18
S. ensifer	13	12–14	6	5–7	17	16–18
S. simulator	13	12–14	6	5–6	17	16–18

2 mm EDTA, pH 7.5). A 100 base-pair (bp) ladder provided molecular weight markers to estimate restriction fragment sizes. Gels were stained with ethidium bromide and photographed on an ultraviolet light transilluminator. Restriction fragments that could not be accurately measured from agarose gels were separated on 8% polyacrylamide gels and stained with SYBR Green I Nucleic Acid Stain™ (Molecular Probes, Eugene, OR) by using a 25-bp ladder for a molecular weight standard. Successful PCR amplification was obtained from 24 of the specimens. A key based on restriction site variation (Li et al., 2006) was used in the identification of the rockfish specimens.

Morphological identification

Some of the pelagic juveniles included in this study could be identified from body and fin pigment patterns and from gross morphological characteristics, whereas others had not yet developed species-specific characters. Meristics used to identify rockfish species included counts of dorsal, anal, and pectoral fin rays (Table 2). Key gross morphological characteristics have been described for *S. jordani* (Moser et al., 1977), *S. levis* (Moser et al., 1977), *S. goodei* (e.g., 35.6-mm-SL specimen illustrated in Sakuma and Laidig [1995]), *S. semicinctus* (Laidig and Adams, 1991), *S. saxicola* (e.g., 38.2-mm-SL specimen illustrated in Laidig et al. [1996]), and *S. auriculatus* (Moser, 1996). However, recently transformed pelagic juveniles of the latter three species do not yet possess distinguishing pigmentation patterns. Those species are included in group 1 in Table 2 and require both morphological and meristic examinations to distinguish them. Although the fin spines of transforming pelagic juveniles are not fully ossified, counts of dorsal-, anal-, and pectoral-fin rays can be made and are useful for separating similarly pigmented species. Body shape, color, and the presence or absence of certain head spines

Table 3

Restriction fragment patterns and consequent species assignments, and species assignments based on morphological features for *Sebastes* spp. examined. Haplotypes a_1 and a_2 are variants of *Mbo* I haplotype a, which was first observed in the present study.

Sample	*Bst*N I	*Bst*U I	*Cfo* I	*Dde* I	*Hind* II	*Hinf* I	*Mbo* I	*Msp* I	*Rsa* I	Genetic assignment	Morphological assignment
1	X		D		A	C	p			*S. semicinctus*	*S. semicinctus*
2	Z		A		A	g	K			*S. hopkinsi* or *ovalis*	*S. hopkinsi*
3	Z		A				K			*S. hopkinsi* or *ovalis*	*S. hopkinsi*
4	Z		A			g	g			*S. hopkinsi*	*S. hopkinsi*
5	Z						g			*S. hopkinsi*	*S. hopkinsi*
8	X						p			*S. semicinctus*	*S. semicinctus*
9	Z									*S. hopkinsi*	*S. hopkinsi* or *semicinctus*
15	Y		D			O	a_1		E	*S. goodei*	*S. goodei*
16	Y		D			O	a_2		E	*S. goodei*	*S. goodei*
17	O	C	D			G	f		C	*S. saxicola*	*S. saxicola*
18	a						c			*S. jordani*	*S. jordani*
19	B					A	q			*S. levis*	*S. levis*
20	Z		A			g	K		C	*S. hopkinsi* or *ovalis*	*S. hopkinsi*
21	c		C	v		a	A		B	*S. rastrelliger*	*S. rastrelliger*
22	F		A	i	C	G	C	a	B	*S. carnatus* or *chrysomelas*	*S. carnatus* or *chrysomelas*
23	F		a	i	C	G	C	a	B	*S. carnatus* or *chrysomelas*	*S. carnatus* or *chrysomelas*
25	F		A	i	C		C	a	B	*S. carnatus* or *chrysomelas*	*S. carnatus* or *chrysomelas*
26	F		D			A	E		C	*S. chlorostictus* or *eos* or *rosenblatti*	*Sebastomus*
27	X		D			C	p			*S. semicinctus*	*S. semicinctus*
31	F		D	v	A	A	k		B	*S. auriculatus*	*S. auriculatus*
44	Z		A	n		g	K		C	*S. hopkinsi*	*S. hopkinsi*
45	Z		A			g	g		C	*S. hopkinsi*	*S. hopkinsi*
48	Z			n			K			*S. hopkinsi*	*S. hopkinsi*
49	X						p			*S. semicinctus*	*S. semicinctus*

(as in the case of *S. auriculatus*) can help to differentiate species with overlapping meristic ranges.

Species that could not be identified from their morphological features were assigned to a complex of species or a subgenus. Group 2 in Table 2 includes species that have similar pigmentation patterns during their pelagic juvenile stage. Meristics and head spination are used to identify *S. atrovirens*. However, the remaining three, *S. carnatus*, *S. caurinus*, and *S. chrysomelas*, are assigned as a species complex because of the uncertainty in identifying the species. The subgenus *Sebastomus* includes ten rockfish species that were found in the collection area and that cannot be distinguished by morphological characters and meristics or by pigmentation.

Results

The way in which the specimens were handled and preserved affected DNA quality and limited the number of genetic and morphological species assignments that could be compared. Only the DNA of seven of the 25 specimens frozen at sea and later thawed and processed was successfully amplified, whereas the DNA of 17 of the 24 specimens preserved in 95% ethanol at the time of capture was amplified. A total of 24 specimens were identified to species or species group based on restriction fragment patterns of the mtDNA using one or more restriction endonucleases (Table 3) and without knowledge of the morphological assignment. Table 4 sum-

Table 4

Developmental stages and counts of dorsal rays, anal rays, and pectoral rays used to assign species to *Sebastes* samples that were independently identified through **genetic analysis.** The number of specimens is given in parentheses. * indicates that the paired fins differed.

Morphological assignment	Genetic assignment	Number of samples	Developmental stage	Number of dorsal rays	Number of anal rays	Number of pectoral rays*
S. auriculatus	*S. auriculatus*	1	juvenile	13	7	18
S. carnatus, chrysomelas, or *caurinus*	*S. carnatus* or *chrysomelas*	3	transforming juvenile (3)	12(2), 13(1)	6(3)	17(3)
S. goodei	*S. goodei*	2	transforming juvenile (1), juvenile (1)	13(1), 14(1)	8(2)	17(2)
S. hopkinsi	*S. hopkinsi*	5	transforming juvenile (2), juvenile (3)	14(2), 15(2), 16(1)	7(5)	17(4), 17/18(1)
S. hopkinsi	*S. hopkinsi* or *ovalis*	3	juvenile (3)	14(1), 15(2)	7(3)	17(3)
S. jordani	*S. jordani*	1	transforming juvenile	14	9	20
S. levis	*S. levis*	1	transforming juvenile	13	6	18
S. rastrelliger	*S. rastrelliger*	1	juvenile	13	6	19
S. saxicola	*S. saxicola*	1	juvenile	12	6	16
subgenus *Sebastomus*	*S. chlorostictus, eos,* or *rosenblatti*	1	juvenile	12	6	18
S. semicinctus	*S. semicinctus*	4	transforming juvenile (2), juvenile (2)	13(4)	7(4)	17(2), 16/17(1), 18(1)
S. hopkinsi or *semicinctus*	*S. hopkinsi*	1	transforming juvenile	14	7	17

marizes the meristic data used to identify species morphologically. When a fish could not be assigned to a species, it was assigned to a species complex or subgenus.

The individuals genetically identified to species were six *S. hopkinsi*, four *S. semicinctus*, two *S. goodei*, one *S. auriculatus*, one *S. jordani*, one *S. levis*, one *S. rastrelliger*, and one *S. saxicola*. The restriction fragment patterns of these juveniles were identical to those of previously observed adult specimens, except for the two *S. goodei* juveniles, each of which differed by a single difference (presumably a site loss in one fish and a site gain in the other) from reference specimens for *Mbo* I (Table 3 and Li et al., 2006). The genetic species assignment of all but one of these specimens matched the identification based on morphological characters (Table 4). The discrepant fish was identified morphologically as either *S. semicinctus* or *S. hopkinsi*. The specimen had 14 dorsal rays, which is within the range of both species (Table 2) and was a transforming pelagic juvenile that had not yet developed the discernible body pigmentation pattern of older juveniles (Table 4).

At the beginning of the study, *S. ovalis* was not included in our database. When we added restriction site information for *S. ovalis* to the database, we found that the species is very similar to *S. hopkinsi* in its haplotype profile. Consequently, three individuals morphologically identified as *S. hopkinsi* were genetically assigned to the complex *S. hopkinsi-S. ovalis*. The restriction enzyme *Dde* I can delineate the two species; however, when we discovered the ambiguity, no samples remained for analysis. Based on meristics, the three specimens are more likely *S. hopkinsi* than *S. ovalis*. The range of counts for fin rays overlaps for the two species (Table 2). However, *S. ovalis* commonly has eight or nine anal rays, and the three specimens in question possessed seven rays that occur commonly in *S. hopkinsi* (Table 4).

Three specimens were assigned to the species complex *S. carnatus-S. chrysomelas-S. caurinus* according to morphological criteria. Haplotype information eliminated *S. caurinus*. Genetic analysis of the one specimen that was morphologically assigned to the subgenus *Sebastomus*, which includes 13 North Pacific species, reduced the possible species to *S. chlorosticus*, *S. eos*, or *S. rosenblatti*.

Discussion

Our results demonstrated that restriction site analysis of mtDNA is a simple and effective tool for identifying juveniles of *Sebastes*

species. The presumed intraspecific variation observed in *S. hopkinsi* and *S. goodei* did not interfere with the application of interspecific variation in species identification, and our other work (Gharrett et al., 2001; Li, 2004) indicates that intraspecific variation generally does not obscure delineation of species. The key we constructed for mtDNA restriction site variation can be especially helpful in learning about variation in the distinguishing morphological characters of the early life stages of *Sebastes*.

One factor that prevented identification of some juvenile specimens was poor DNA quality. Specimens must be properly preserved to provide high quality DNA for genetic analysis. Our success in amplifying DNA from specimens preserved in several volumes of 95% ethanol immediately after capture was substantially higher than that of specimens that had been frozen after capture and subsequently thawed for morphological studies.

Several small groups of species had similar restriction site patterns. Consequently, there was ambiguity in the genetic analysis of those groups. Specifically, we were unable to separate *S. carnatus* from *S. chrysomelas*, and we were unable to distinguish among *S. chlorostictus*, *S. eos*, and *S. rosenblatti*. However, morphological characteristics could not reveal a difference between *S. carnatus* and *S. chrysomelas*, nor could they distinguish any of the 13 *Sebastomus* species, including *S. chlorostictus*, *S. eos*, and *S. rosenblatti*.

Sebastes carnatus and *S. chrysomelas* are very closely related and, as adults, differ morphologically only in body coloration. *Sebastes carnatus* has flesh-colored blotches on an olive-brown background, and *S. chrysomelas* has yellow blotches on a black background (Love et al., 2002). They are found across similar geographic ranges, from northern California to Baja California, and are often sympatric, inhabiting rocky substrates, although they have different depth distributions (Larson, 1980), and their segregation is maintained by the social dominance of *S. chrysomelas* (Larson, 1980; Hoelzer, 1987). The two species may also differ slightly in gill-raker counts: *S. carnatus* typically has 28–30, and *S. chrysomelas* typically has 27–28 (Hallacher and Roberts, 1985). Their taxonomic status as distinct species is generally recognized from their different colorations, even though no fixed biochemical or genetic differences have been reported (Seeb, 1986; Seeb and Kendall, 1991; Hunter, 1994; Alesandrini, 1997). A recent study with the use of microsatellites in the nuclear DNA and mtDNA sequence variation has provided evidence that the two species *S. carnatus* and *S. chrysomelas* are genetically divergent (Narum, 2000).

Sebastes chlorostictus, *S. eos*, and *S. rosenblatti* are also morphologically similar, are present sympatrically, and are closely related (Chen, 1971; Love, 1996; Rocha-Olivares et al., 1999; Love et al., 2002). As adults, these species segregate by depth to some extent; *S. rosenblatti* occupies a somewhat narrower range than the other two (Love et al., 1990). Cladistic analyses indicate that *S. rosenblatti* is the most ancient of the three species (Rocha-Olivares et al., 1999). Estimates of divergence times of the subgenus *Sebastomus* may indicate that the three species are the result of the most recent speciation events within the subgenus, which may have begun less than 140,000 years ago (Rocha-Olivares et al., 1999).

The assignment of four specimens to multispecies groups in this study indicates the need for further effort to develop markers that will delineate the species in question. Approaches include screening additional regions of the mtDNA and application of additional restriction enzymes. If additional mtDNA regions and restriction enzymes do not provide species-specific information, other molecular techniques, such as the use of microsatellites, should be considered.

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Potential use of offshore marine structures in rebuilding an overfished rockfish species, bocaccio (*Sebastes paucispinis*)

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Abstract—Although bocaccio (*Sebastes paucispinis*) was an economically important rockfish species along the west coast of North America, overfishing has reduced the stock to about 7.4% of its former unfished population. In 2003, using a manned research submersible, we conducted fish surveys around eight oil and gas platforms off southern California as part of an assessment of the potential value of these structures as fish habitat. From these surveys, we estimated that there was a minimum of 430,000 juvenile bocaccio at these eight structures. We determined this number to be about 20% of the average number of juvenile bocaccio that survive annually for the geographic range of the species. When these juveniles become adults, they will contribute about one percent (0.8%) of the additional amount of fish needed to rebuild the Pacific Coast population. By comparison, juvenile bocaccio recruitment to nearshore natural nursery grounds, as determined through regional scuba surveys, was low in the same year. This research demonstrates that a relatively small amount of artificial nursery habitat may be quite valuable in rebuilding an overfished species.

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Beginning in 1995, annual surveys of fish assemblages at oil and gas platforms and natural reefs throughout southern California were conducted with a research submersible (summarized in Love et al., 1999, 2000, 2003). Many California oil and gas platforms harbor three fish assemblages: those that occupy the shell mound area surrounding the base of the platform; those that occupy the waters adjacent to the platform bottom, and those that occupy the midwater. Rockfishes (genus *Sebastes*), of about 35 species, dominate these assemblages. The shell mound assemblage is composed primarily of juvenile rockfishes, dwarf rockfishes, and other species; the platform bottom assemblage is composed of adult and subadult fishes; and the midwater assemblage of most platforms (and the bottoms of some mid-depth platforms) is dominated by young-of-the-year (YOY) and older juvenile rockfishes that comprise at least 28 species. These fishes are rarely more than 20 cm long (total length). In the midwaters of most California platforms, there are only low densities of predatory reef fish species, such as kelp bass (*Paralabax clathratus*) and cabezon (*Scorpaenichthys marmoratus*), or semipelagic, large predatory species, such as Pacific barracuda (*Sphyraena argentea*) and yellowtail (*Seriola lalandi*). The proper disposition of the approximately 6000 marine offshore oil and gas platforms and associated structures now in service worldwide is in dispute. There are 27 platforms off California and, as in other parts of the world, there is considerable debate over the ultimate fate of these structures once they are uneconomical to operate (Schroeder and Love, 2004). In this article, we focus on the role that some artificial structures play as rockfish nursery habitat off California.

During some years, we have noted particularly high densities of YOY bocaccio (*Sebastes paucispinis*), widow (*S. entomelas*), squarespot (*S. hopkinsi*), and blue (*S. mystinus*) rock-

Figure 1

Examples of young-of-the-year (YOY) and other juvenile fishes found in high densities at platform Gilda, October 2003. (**A**) YOY bocaccio (*Sebastes paucispinis*); (**B**) a YOY lingcod (*Ophiodon elongatus*); (**C**) one-year-old vermilion rockfish (*Sebastes miniatus*).

fishes around a number of these platforms. Similar high densities of young rockfishes were noted in the late 1950s at two nearshore platforms off Santa Barbara (Carlisle et al., 1964). The densities of YOY rockfishes are usually higher at platforms than at most natural outcrops (Schroeder et al., 2000; Love et al., 2003). As on natural outcrops, however, YOY rockfish recruitment to platforms is highly variable from year to year.

In 2003, while conducting fish surveys around eight oil platforms in southern California, we observed high densities of YOY rockfishes (e.g., bocaccio and widow rockfish), YOY lingcod (*Ophiodon elongatus*), and one-year-old vermilion rockfish (*S. miniatus*) (Fig. 1). Given the uncertainty regarding the role that platforms might play as fish habitat, we were interested in understanding how important young bocaccio, and by extension the platforms, might be to the stock and populations of this species in the region. Because of the severely overfished status of bocaccio and because a stock assessment model had been developed by NOAA Fisheries, we focused our attention on this species.

Along the Pacific Coast of North America, bocaccio have been reduced to about 7.4% of their unfished population (MacCall[1]). Bocaccio are relatively long-lived (to over 50 years) and have extremely variable annual juvenile recruitment success; over natural outcrops, large year classes are found about once a decade (Tolimieri and Levin, 2005). YOY bocaccio settle from a juvenile micronektonic stage to shallow high-relief habitats (such as kelp beds) and usually migrate into deeper waters within one year. Historically, the species was abundant from Oregon to at least northern Baja California (Love et al., 2002).

In this article we focus on the large recruitment of YOY bocaccio observed at platforms in the Santa Barbara Channel in 2003. We estimate the minimum number of YOY bocaccio at eight platforms in the Santa Barbara Channel, southern California, and estimate the contribution these juveniles may make (as surviving adults) to the rebuilding of the overfished stock. We also compare the densities of YOY bocaccio around the platforms with those determined during the same year in studies on natural reefs throughout southern, and parts of central, California.

Material and methods

Between 10 and 15 October 2003, we surveyed the jacket (horizontal beams and vertical supports)

[1] MacCall, A. D. 2003. Status of bocaccio off California in 2003. *In* Status of the Pacific coast groundfish fishery through 2003 stock assessment and fishery evaluation (vol. 1), v + 56 p. Pacific Fishery Management Council, 7700 NE Ambassador Place, Suite 200, Portland, OR 97220.

of eight platforms in the Santa Barbara Channel (Fig. 2) using the *Delta* research submersible, a 4.6-meter, 2-person vessel operated by Delta Oceanographics of Oxnard, California. In the platform midwater, we conducted surveys along each of the platform's horizontal beams, located at 20- to 30-m intervals between near-surface waters and the bottom. The shallowest beams were situated at depths of 15–34 m; thus the uppermost parts of the platform were not surveyed. On the seafloor, fish surveys were conducted next to the platform bottom and over the shell mounds that surround platforms. Because of poor water visibility, we were unable to survey either the platform bottoms or the shell mounds of four platforms (i.e., A, B, C, and Hillhouse). We conducted belt transects on the shell mound at an average distance of approximately 7.75 m from the platform and around the platform base and horizontal beams at a distance of approximately 2 m from the platform, while the submersible maintained a speed of about 0.5 knots. Divers estimated transect lengths by first estimating velocity over a short course, using twin laser beams as an aid to estimate their lengths. Submersible surveys were conducted during daylight hours between one hour after sunrise and two hours before sunset. During each transect, the researcher made observations from a viewing port on the starboard side of the submersible. An externally mounted hi-8-mm video camera with associated lights filmed the same viewing fields as seen by the observer. Images recorded by the camera were laid down on tape. The observer identified, counted, and estimated the lengths of all fishes and verbally recorded those data on the videotape. All fishes within two meters of the submersible were counted. Fish lengths were estimated by using a pair of parallel lasers mounted on either side of the external video camera. The projected reference points were 20 cm apart and were visible both to the observer and in the video camera image. We assumed that bocaccio 20 cm or less were YOY, in accordance with growth studies of bocaccio.

Many years of experience along the Pacific Coast have shown that if the *Delta* is moving at a constant and slow rate of speed, as in these surveys, there is very little obvious effect on most fishes, particularly rockfishes (M. Love[2]; O'Connell[3]; Yoklavich[4]). Certainly, we noticed virtually no movement from most of the fishes in our study as the research submersible passed by. Unless hidden in complex substrate, fishes as small as about 5 cm in length are readily visible within two meters of the submersible.

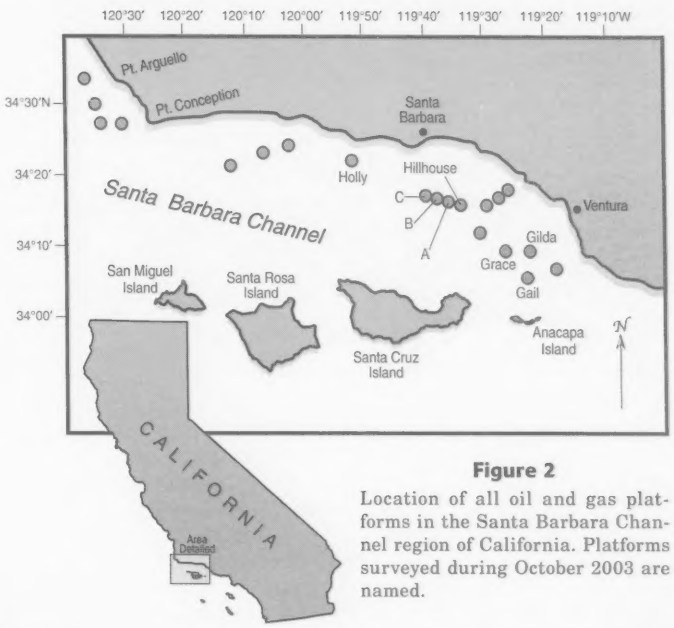

Figure 2

Location of all oil and gas platforms in the Santa Barbara Channel region of California. Platforms surveyed during October 2003 are named.

Using the data from these surveys, we computed the densities (number of fish per m^2) of YOY bocaccio at the midwater horizontal beams, bottom (when surveyed), and shell mounds (when surveyed) of each platform. From these density estimates, we calculated the abundance of YOY bocaccio at each platform (for protocols see Love[5]).

These abundance estimates are conservative for four reasons. First, we conducted the platform surveys about two meters from the platform and our belt transects count only those YOY bocaccio within two meters of the submersible. Particularly in platform midwaters, densities of YOY rockfishes tend to be lower outside the platform framework (the zone traversed by the submersible) than inside. Second, beginning a few months after settling on platforms, the more open water species, such as bocaccio, blue, widow, squarespot, and yellowtail rockfishes, become less closely associated with structure. There appears to be an ontogenetic shift away from a close association with habitat to a wider association, where these fish wander away from the immediate vicinity of the platform. This shift is particularly true during years with high densities (as in 2003), when large schools wander freely within the relatively open waters of the platform jacket. Third, as noted above, at each

[2] Love, M. 2002. Unpubl. data. Marine Science Institute, University of California, Santa Barbara, CA, 93160.

[3] O'Connell, V. 2004. Personal commun. Alaska Department of Fish and Game, 304 Lake St. Room 103 Sitka, AK 99835.

[4] Yoklavich, M. 2004. Personal commun. NOAA/NMFS Santa Cruz Laboratory, 110 Shaffer Road Santa Cruz, CA 95060.

[5] Love, M. 2005. Methods used to estimate abundance in numbers of young-of-the-year (YOY) bocaccio. Website: http://www.id.ucsb.edu/lovelab [accessed on 26 September 2005].

platform we did not survey in the midwaters above the shallowest horizontal beam (at depths of 15–34 m). Thus, some of the potential bocaccio nursery grounds were not sampled. Fourth, for those platforms where visibility was too poor for us to sample the bottom or shell mound (A, B, C, and Hillhouse), we estimated YOY bocaccio abundances only for that part of the platform (the midwater) that could be surveyed. However, although visibility was too poor to conduct operations on the bottom, we could see high densities of bocaccio inside the platform below the submersible at several platforms when we conducted midwater surveys. Thus, on these platforms, it is highly likely that the YOY bocaccio aggregation extended well below the level of our surveys and that these aggregations contained substantially more of these fishes than we estimated.

We also estimated the level of recruitment of YOY bocaccio in 2003 to natural reefs using data from a variety of sources. In this overview, we included 1) our submersible surveys conducted at depths at which YOY bocaccio may reasonably recruit (down to about 100 m), 2) a scuba survey conducted by D. M. Schroeder, and 3) data from nearshore rocky reef fish surveys conducted by other researchers. The latter surveys were conducted by using scuba at depths of 25 m or less.

Table 1

Densities of young-of-the-year bocaccio (*Sebastes paucispinis*) at eight platforms in the Santa Barbara Channel, October 2003. Because of poor visibility, the zones of some platforms were not surveyed; these are marked N/A.

Platform	Platform zone surveyed	Depth (m)	Number of fish	Density (fish/100 m^2)
A	midwater	15	0	0
		32	0	0
	no base or shell mound	N/A	N/A	N/A
B	midwater	20	0	0
		30	13	4.8
		40	165	57.7
	no base or shell mound	N/A	N/A	N/A
C	midwater	20	0	0
		30	62	17
		45	127	32.1
	no base or shell mound	N/A	N/A	N/A
Gail	midwater	32	2	0.6
		47	27	6.7
		69	18	4.1
		90	3	0.8
		111	25	5.6
		138	1	0.2
		164	1	0.2
		195	4	0.7
	base	226	0	0
	shell mound	226	0	0
Gilda	midwater	25	55	13
		42	24	6.2
	base	62	1023	242.4
	shell mound	62	1078	169.6
Grace	midwater	26	4006	476.8
		45	1537	193.1
		68	1124	258
		70	845	171
		80	92	221.5
	base	96	13	2.6
	shell mound	96	0	0
Hillhouse	midwater	20	0	0
		35	506	140
	no base or shell mound	N/A	N/A	N/A
Holly	midwater	34	18	4
	base	60	12	2.1
	shell mound	60	4	0.4
Total			10,785	

Results

YOY bocaccio were observed at seven of the eight platforms we surveyed. We observed a total of 10,785 YOY bocaccio in the survey (Table 1). We saw no YOY bocaccio at depths of 20 m and less, none at 226 m, and relatively high densities at depths between about 25 and 80 m. Mean YOY bocaccio densities varied between platforms. Platform Grace (368.0 fish/100 m^2) and Gilda (95.2 fish/100 m^2) harbored the highest densities, whereas no YOY bocaccio were observed at Platform A (Fig. 3). Using the methods detailed in Love,[5] we estimated that there was a minimum of 433,682 YOY bocaccio at the seven platforms (Table 2).

Using the model STATC (details of the model are given in MacCall[1]), which is the current basis for fishery management under the Pacific Fisheries Management Council, we determined that the 433,682 YOY bocaccio living around these platforms constitute about 20% of

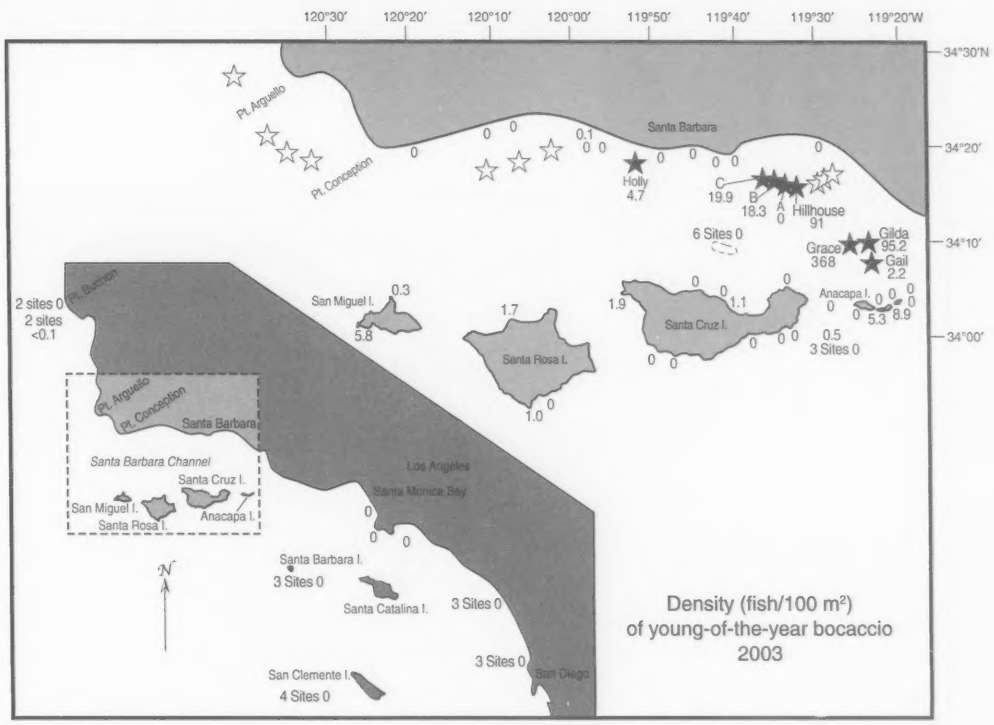

Figure 3

Densities of YOY bocaccio (*Sebastes paucispinis*) (fish/100 m^2) in southern and parts of central California in 2003. Surveys were conducted at sites that were likely YOY bocaccio recruitment habitats, primarily at nearshore kelp beds and rocky outcrops. Surveys by M. Love were conducted from the research submersible *Delta*; the others were conducted by scuba divers. The open stars represent platforms that were not surveyed; the closed stars represent platforms that were surveyed.

the average yearly value, and 40% of the median value for the entire range of the species (based on YOY estimated abundances between 1990 and 2003). From the same model, we estimated that these young fish will eventually contribute slightly less (0.8%) than one percent of the additional amount of fish needed to rebuild the Pacific Coast stock.

By comparison with most of the platforms we surveyed, there was low or no YOY bocaccio recruitment to natural reefs in southern and parts of central California during 2003 (Fig. 3). During 2003, surveys were conducted at 64 sites and no YOYs were observed at 50 of these reefs; most of the other 14 sites harbored very low densities. The highest density noted at any natural outcrop (8.9 fish/100 m^2), observed at a small kelp bed at Anacapa Island, was much lower than that at five of the surveyed platforms.

Table 2

Estimated numbers of young-of-the-year bocaccio (*Sebastes paucispinis*) inhabiting eight platforms in the Santa Barbara Channel, 2003. Note that the surveys of four platforms, Hillhouse, C, B, and A, did not include the bottom of the platform and its surrounding shell mound.

Platform name	Estimated abundance
Grace	353,411
Gilda	39,854
Hillhouse (partial)	22,171
C (partial)	5977
B (partial)	5911
Gail	5521
Holly	837
A (partial)	0
Total	433,682

Discussion

According to our estimates, the YOY bocaccio living around seven platforms in the Santa Barbara Channel were important to the regional bocaccio population, and it appears that a substantial portion of the YOY bocaccio

recruitment that occurred in the Santa Barbara Channel during 2003 took place at the surveyed platforms.

Because it is likely that most reefs both attract and produce fishes, discussions of reef function have evolved from the single issue of attraction versus production to an evaluation of the ecological performance of fishes at natural and human-made habitats. Reviews and studies that compare natural and human-made reefs as juvenile fish habitats should address: 1) a comparison of the survival rate of young fishes (including predation, growth rates, and survival after emigration, if that occurs) at the two habitat types, 2) the density of recruiting juveniles at a human-made reef versus that at surrounding natural reefs, 3) the possibility that a human-made reef is drawing recruiting juvenile fishes from nearby natural reefs, 4) the source of juvenile fishes found on a human-made reef—either from the plankton or from natural reefs (discussed in a number of papers including Bohnsack et al., 1994; Carr and Hixon, 1997; Pickering and Whitmarsh, 1997).

What is the survival rate of young fishes that recruit from the plankton to platforms and those that recruit to natural reefs? What appears to be a unique feature of the midwaters of many California platforms (compared to both natural reefs and to Gulf of Mexico platforms) is that many may act as juvenile (particularly YOY) fish refuges. The midwaters of platforms do not act as structural refuges. That is, they are not dotted with crevices, caves, and other complexities that allow fish to hide (Hixon and Beets, 1993). Rather, platforms may afford spatial refuges because, in general, concentrations of adult reef fishes tend to be found at the bottom of platforms (except for those platforms that harbor almost no adult fishes at all) rather than in the midwaters. Transitory and migrating piscivorous species, such as jacks and barracuda (taxa that are abundant around Gulf of Mexico platforms [Stanley and Wilson, 2000]) are also not common around most California platforms (Love et al., 2003). We have also not observed high densities of either fish-eating pinnipeds or sea birds around these structures. In addition, studies (Schroeder et al., 2005) demonstrate that predation rates on small fishes are lower in platform midwaters than at natural reefs.

Several lines of evidence demonstrate that YOY bocaccio recruit to platforms from the plankton and that the platforms do not attract previously settled fish from natural reefs. Studies of the seasonal timing of platform recruitment pulses and the size of the recruiting individuals are consistent with the hypothesis that young bocaccio settle on the platforms from the pelagic environment (Nishimoto et al., 2005; Schroeder[6]; Nishimoto[7]). Are these platforms, then, drawing away pelagic juveniles that would have settled instead on natural outcrops? Although it is possible that some pelagic juveniles that had settled on platforms would have found natural reefs, it is likely that most of these fish would not have survived in the absence of these structures. As an example, Emery et al. (2006) simulated near-surface drift trajectories from high-frequency radar current measurements to model movements of pelagic juvenile bocaccio in the vicinity of a platform off Pt. Arguello, central California. They estimated that for 1999 and 2002, a minimum of 76% and 69% of the modeled pelagic juvenile bocaccio would not have found natural habitat on which to settle. Although the platforms we surveyed were east of the platform examined in the Emery et al. (2006) study, it is unreasonable to conclude that these relatively small platforms are filtering the majority of pelagic juvenile bocaccio from the pelagic environment to the exclusion of natural reefs. Rather, it is possible that some platforms provide recruitment habitat for fishes that would otherwise be lost from the population.

What is the fate of YOY bocaccio that settle around platforms? In general, YOY bocaccio emigrate from shallower platforms within two years. At least some of these fish migrate to natural reefs, because young bocaccio tagged around Platforms A and B in 1978 and 1979 were recaptured on natural reefs as adults as much as 150 km from the tagging sites (Hartman, 1987). Our observations of bocaccio on the deeper Platform Gail demonstrate that many of the YOY bocaccio that recruited to that platform from the plankton in 1999 remained in the area (migrating to the bottom in 2000) and matured into adults (Fig. 4).

To summarize, the weight of evidence implies that some of the platforms in southern California produce bocaccio. During some years, young bocaccio settle from the plankton to the platforms in large numbers. This settlement may occur even when juvenile recruitment to natural reefs in the same region is low. Compared to the structure of most natural reefs, the structural complexity and high vertical profile of platforms probably provide pelagic juvenile rockfishes with a relatively strong stimulus to trigger settlement. Mortality on platform YOY bocaccio from predation may be relatively low because of a relative scarcity of predators. There is also evidence that platforms retain pelagic bocaccio juveniles that would otherwise have been carried into inhospitable offshore waters. At least some bocaccio that emigrate from platforms survive to populate natural reefs, whereas, as in the case of one platform, some YOY bocaccio remain and mature into adults. Thus, there is the likelihood that many of the YOY bocaccio we observed at platforms will either emigrate and seed natural reefs or will reside at the platforms and reproduce.

Clearly, our research was subject to a number of assumptions and the ambiguities that may be associated with these assumptions. These assumptions add some degree of uncertainty both to our estimates of YOY bocaccio abundances and their subsequent contribution to stock rebuilding. However, we consider this research to be sufficiently strong to demonstrate the importance of

[6] Schroeder, D. M. 2002. Unpubl. data. Marine Science Institute, University of California, Santa Barbara, CA 93106.

[7] Nishimoto, M. 2005. Personal commun. Marine Science Institute, University of California, Santa Barbara, CA 93106.

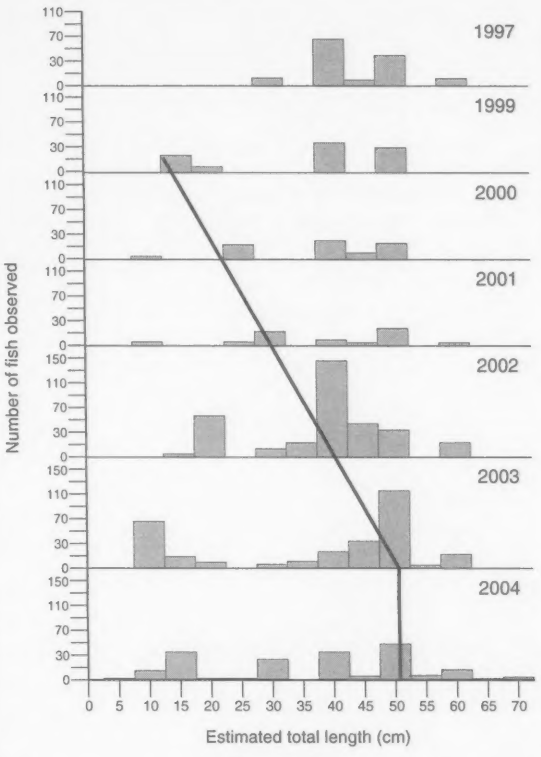

Figure 4

Size-frequency histogram of all bocaccio (*Sebastes paucispinis*) observed in all depths at Platform Gail from the research submersible *Delta*, 1995 to 2004. A relatively strong year class recruited in 1999 to the platform midwaters. We observed these fishes at the bottom in 2000 and they remained there through 2004. The near cessation of growth of these fishes between 2003 and 2004 approximates the size at which 100% of the fish are mature (Love et al., 2002).

spatial structure in driving marine population dynamics, where a small amount of nursery habitat, either human-made or natural, may disproportionately impact a widely distributed species. It also highlights the importance of understanding the potential role of any marine habitat before that habitat is altered, either purposefully or unintentionally.

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Do oil and gas platforms off California reduce recruitment of bocaccio (*Sebastes paucispinis*) to natural habitat? An analysis based on trajectories derived from high-frequency radar

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Abstract—To investigate the possibility that oil and gas platforms may reduce recruitment of rockfishes (*Sebastes* spp.) to natural habitat, we simulated drift pathways (termed "trajectories" in our model) from an existing oil platform to nearshore habitat using current measurements from high-frequency (HF) radars. The trajectories originated at Platform Irene, located west of Point Conception, California, during two recruiting seasons for bocaccio (*Sebastes paucispinis*): May through August, 1999 and 2002. Given that pelagic juvenile bocaccio dwell near the surface, the trajectories estimate transport to habitat. We assumed that appropriate shallow water juvenile habitat exists inshore of the 50-m isobath. Results from 1999 indicated that 10% of the trajectories represent transport to habitat, whereas 76% represent transport across the offshore boundary. For 2002, 24% represent transport to habitat, and 69% represent transport across the offshore boundary. Remaining trajectories (14% and 7% for 1999 and 2002, respectively) exited the coverage area either northward or southward along isobaths. Deployments of actual drifters (with 1-m drogues) from a previous multiyear study provided measurements originating near Platform Irene from May through August. All but a few of the drifters moved offshore, as was also shown with the HF radar-derived trajectories. These results indicate that most juvenile bocaccio settling on the platform would otherwise have been transported offshore and perished in the absence of a platform. However, these results do not account for the swimming behavior of juvenile bocaccio, about which little is known.

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Fish. Bull. 104:391–400 (2006).

The 27 oil and gas platforms off southern and central California have limited life spans. Many of these structures have been in place for over 20 years (Love et al., 2003), and it is expected that some of these platforms will be decommissioned in the near future. Because decommissioning may entail full removal of the platform, agency personnel tasked with determining the best course of action in regard to the platforms would likely benefit from an understanding of the role that platforms play as fish habitat (Schroeder and Love, 2004).

The platforms harbor high densities of many species of fishes, although species compositions vary with platform bottom depth (Love et al., 1999a; 1999b; Love et al., 2003). About 35 species of rockfishes (genus *Sebastes*) dominate the three distinct assemblages found around many platforms in the Santa Barbara Channel and off central California: the bottom, shell mound, and midwater assemblages. Fishes around platform bottoms tend to be adult and subadult individuals. Those on the shell mounds are usually adults of dwarf species or juveniles of larger taxa. The midwater assemblages are composed almost entirely of juvenile fishes. Some of these juvenile fishes are one and two-year old individuals, but most are young-of-the-year (YOY) rockfishes. Densities of YOY rockfishes around platforms are usually far higher than those at nearby natural reefs (Love et al., 2003). These observations have raised a concern (e.g., Krop[1].) that platforms

[1] Krop, L. 1997. Environmental user group representative, disposition panel. *In* Proceedings: Public workshop, decommissioning and removal of oil and gas facilities offshore California: recent experiences and future deepwater challenges, September 1997 (F. Manago, and B. Williamson, eds.), p 172. Mineral Management Service OCS Study 98-0023. Coastal Research Center, Marine Science Institute, Univ. California, Santa Barbara, California, 93106. MMS Cooperative Agreement Number 14-35-0001-30761.

may reduce recruitment to natural reefs by functioning as catchments for pelagic juvenile rockfishes.

To investigate the possibility that an oil platform may reduce recruitment of rockfishes to natural habitat, we simulated drift pathways (hereafter referred to as "trajectories") from an existing platform to nearshore habitat using current measurements from high-frequency (HF) radars.

Materials and methods

Species modeled

Because trajectories derived from HF radar approximate transport pathways of near surface water parcels, we chose to model the movements of pelagic juvenile bocaccio (*Sebastes paucispinis*) that dwell near the surface during their time in the plankton. This historically important recreational and commercial fishing target in central and southern California (Love et al., 2002), is also among the shallowest dwelling juvenile fishes (Lenarz et al., 1991; Ross and Larson, 2003).

Off central and northern California, parturition for bocaccio occurs from January to May and peaks in February (Love et al., 2002). Off southern California, the species has a reproductive season that spans all year, but most larvae are released from October to July, although January is the peak month. Juvenile bocaccio recruit to inshore waters from February to August off central California, although May through July is the peak season (Love et al., 2002). The trajectory simulation period from May through August was chosen to span this principal recruitment season.

Bocaccio range from the Alaska Peninsula to central Baja California, and adults are usually found over high relief boulder fields and rocks in 50–250 m of water (Love et al., 2002). The fish most often settle in rocky habitat covered with various algae or in sandy zones with eelgrass. Juvenile bocaccio are commonly found in drifting kelp (Mitchell and Hunter, 1970; Boehlert, 1977) indicating that the fish recruit to natural habitat encountered in offshore surface waters. For this analysis, we assumed that waters from the shallow subtidal to the 50-m isobath represented suitable habitat for juvenile recruits. This choice reflects the lack of information about suitable habitat locations in our study area and likely results in overestimates of the abundance of such habitat.

Annual scuba surveys and submersible surveys (1995–2001) in the Santa Barbara Channel and Santa Maria Basin regions showed that YOY bocaccio inhabit the upper 35 m around one or more platforms for each year surveyed. Platform Irene (34°36.62′N, 120°43.40′W; bottom depth 73 m) was selected for analysis because fish recruited to it each year from 1995–2001 (Love et al., 2001) and it was the site of the highest density of YOY bocaccio observed from submersible surveys during these years (Love et al., 2003). Moreover, from May through August, 1999 and 2002, Platform Irene was also in a region of good HF radar coverage, which allowed computation of extensive trajectory ensembles.

Ocean current measurement and trajectory calculation

Near-surface ocean currents were measured hourly by using an array of three HF radars (SeaSondes, manufactured by CODAR Ocean Sensors, Ltd. of Los Altos, CA) operating at 12–13 MHz. At these frequencies, the measurement is an average over the upper 1 m of the water column (Stewart and Joy, 1974). The radars were located at Pt. Sal, Pt. Arguello, and Pt. Conception (Fig. 1A). HF radars measure components of surface currents by means of a Doppler technique, at spatial increments of 1.5 km in range and 5° in azimuth from the radar location. Surface current vectors in an east-north coordinate system were computed on a 2-km grid by using the least square technique described by Gurgel (1994). With this technique, all current components obtained within a 3-km radius around each grid point were combined to estimate the surface current every hour. The 3-km radius limits the spatial resolution of the near-surface current fields. Emery et al. (2004) have described the processing of the HF radar data in more detail. Further discussion on the use of HF radars for measuring near surface currents is given by Paduan and Rosenfeld (1996) and Graber et al. (1997).

Emery et al. (2004) assessed performance of the three HF radars by comparing them with *in situ* current meters at 5 m depth. They found that root-mean-square differences in radial speed measurements between HF radars and current meters ranged from 0.07 to 0.19 m/s. Recent observations comparing surface currents from HF radars and drifters have indicated that differences are substantially reduced if spatial variability in current fields is accounted for (Ohlmann, 2005).

The areas used for computing trajectories were offshore of Pt. Conception and Pt. Arguello as shown in Fig. 2A for 1999 and Fig. 3A for 2002. These areas were selected to maximize the spatial coverage, and to minimize the inclusion of grid points with low temporal coverage. Variable coverage from individual radars results in differences in coverage between years. Boundaries of nominal coverage areas were oriented along and perpendicular to isobaths. Platform Irene is about 2 km from the inshore boundaries, which lie along the 50-m isobath (Figs. 2A and 3A). At times actual radar coverage exceeded nominal coverage boundaries as may be seen by comparing sample computed trajectories (black lines, Fig. 1A) with the 2002 boundary (gray closed curve, Fig. 1A). Coverage in 2000 and 2001 for May through August was inadequate for producing trajectory ensembles around Platform Irene.

A new trajectory was begun at the location of Platform Irene every 4 hours from 1 May through 31 August for 1999 and 2002. Positions along the trajectories were determined by integrating current vectors forward in time using a fourth order Runge-Kutta algorithm. Trajectories ended where they encountered spatial gaps or where they reached the edge of radar coverage.

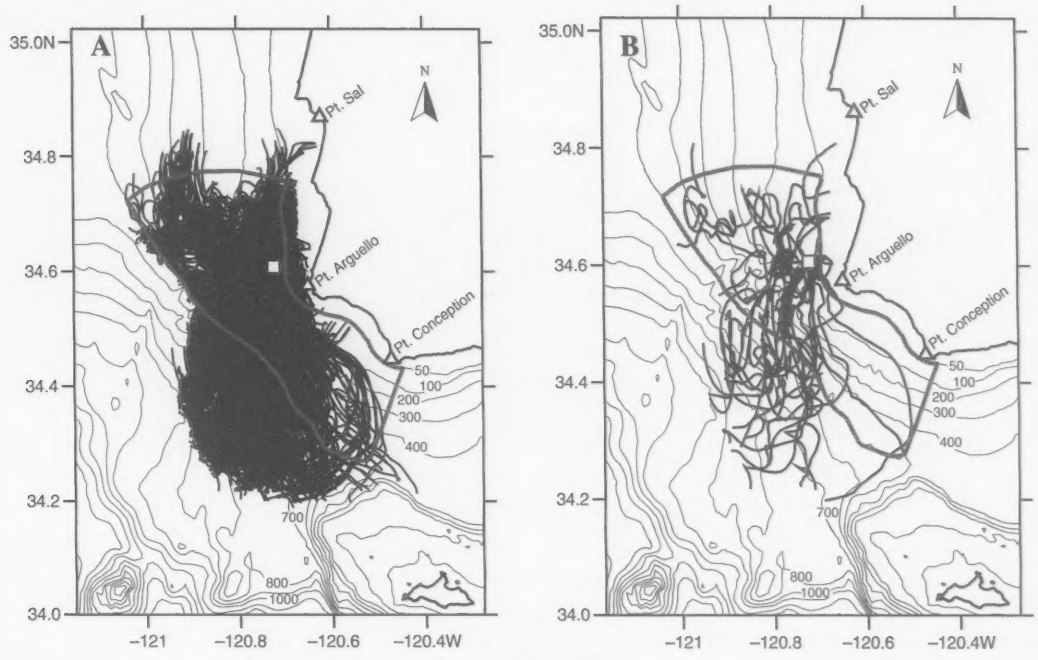

Figure 1

(**A**) Map of study area near Pt. Conception, California, showing trajectories derived from high-frequency (HF) radar from 1 May–31 Aug 2002. Triangles show HF radar locations and the white square shows Platform Irene. Gray curve superimposed on trajectories is the coverage boundary used for 2002. Labeled thin black lines are bathymetric contours. (**B**) Heavier black lines are 25 sample trajectories that intersect the coverage boundary. Gray curve is the same as in panel A. The trajectories in panels A and B were created from velocity time series that were interpolated with empirical orthogonal functions (EOFs).

The number of trajectories reaching the coverage boundaries defined in Figures 2A and 3A were reduced by gaps in spatial and temporal radar coverage. For example, of the 670 possible trajectories in 2002, 541 (81%) ended within the radar coverage area and 129 (19%) intersected the coverage boundary. Changes in spatial coverage on diurnal and longer time scales resulted from several factors, such as broadcast interference, and are a characteristic of HF radars (Paduan and Rosenfeld, 1996). Gaps in the velocity time series were also caused by outages of individual radars. The average durations of these gaps were 4.4 ±22.3 h and 5.9 ±7.9 h in 1999 and 2002, respectively. Outages of individual radars also produced a few long gaps in the velocity time series for each year across the entire coverage area. In 1999 two long gaps occurred: one from 1800 coordinated universal time (UTC) 28 June through 2000 UTC 22 July, and a second from 2300 UTC 24 July through 2200 UTC 13 August. In 2002 a single long gap occurred from 1700 UTC 16 May through 0100 UTC 21 May. These longer gaps were not filled.

Shorter gaps were filled by interpolation by using empirical orthogonal functions (EOFs; (Emery and Thomson, 1998)). EOFs incorporate the underlying spatial structure of all velocities recorded at all locations where data existed at a given time. Any velocity component, u say, at grid point j may be expressed as

$$u_j(t) = \sum_{i=1}^{N} a_i(t)\varphi_{ij} + \bar{u}_j, \quad (1)$$

where t = time;
$\bar{u}_j$ = the time average at location j (computed from available data at location j);
a_i = the time-varying amplitude function;
φ_{ij} = the ith spatial EOF mode at location j; and
N = the number of modes.

The first seven modes (i.e., N=7) were used for interpolation and explained 64% (1999) and 56% (2002) of the variance. EOF interpolation increases the number of trajectories reaching the coverage boundary to 99%. As a test, gaps were also filled with linear, spline, and moving average interpolation, but EOF interpolation resulted in the most trajectories reaching the coverage boundaries. Otherwise, results did not depend strongly on the interpolation method.

The fraction of filled data with EOF interpolation compared with the total possible data was 4% in 1999,

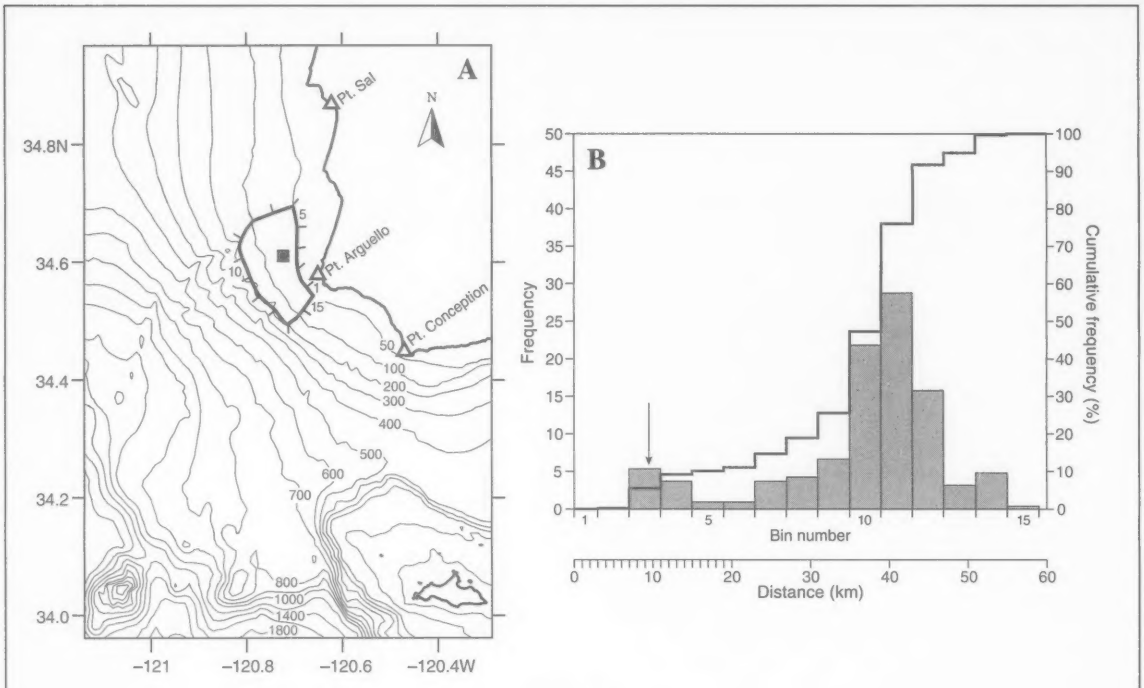

Figure 2

(**A**) Coverage boundary (indicated by heavy lines around the black square [Platform Irene]) for 1 May–31 August 1999. Numbers and tick marks around boundary identify bins corresponding to x-axis in panel B. (**B**) Histogram (gray bars, left-hand scale) and cumulative frequency (bold line, right-hand scale) show fraction of trajectories (in percent) intersecting bins around coverage boundary. Panel A shows bin locations. Distance around the coverage boundary (Fig. 2A) in kilometers is also shown (bottom scale). Arrow above histogram shows boundary location nearest Platform Irene.

12% in 2002, and 14% with the 2002 data for the 1999 coverage boundary. Here the total possible data were the number of grid points within the coverage boundary for either 1999 (45 grid points) or 2002 (291 grid points) multiplied by the number of hours between 1 May and 31 August minus the long gaps discussed above (2952 hours–1057 hours in 1999, 2952 hours–104 hours in 2002). Examples of 25 EOF-filled trajectories that started every 120 hours and intersected the 2002 coverage boundary are shown in Figure 1B.

The principal quantity used in our study to estimate how Platform Irene might affect transport to nearshore habitat was the histogram of points where trajectories crossed the boundaries of the coverage areas. To determine this quantity, coverage boundaries were divided into 4-km-long segments, or bins. The first bin of each histogram was less than 4 km because distances around the coverage boundaries were not exactly divisible by 4. Bin numbers increased counter-clockwise around the boundaries starting from 1 in the southeastern corner (Figs. 2A and 3A). The smallest numbers identified bins lying along the 50-m isobath.

Results

Trajectories originating at Platform Irene were sufficiently dense to fill in much of the surrounding area. In 2002 for example, EOF-filled trajectories spread over an area of about 20 km in the cross-shore direction by 60 km in the alongshore direction (Fig. 1A). North of Pt. Arguello, several trajectories crossed the 50-m isobath and some ended very near shore. South of Pt. Arguello, only a few trajectories approached the 50-m isobath. Instead, most turned southward or southwestward and moved offshore. A tendency for trajectories to align parallel to isobaths was evident in the northern end of the ensemble, although in other areas, such as the southeast, many trajectories lay across isobaths.

A histogram of points where trajectories crossed the coverage boundary for May–August 1999 exhibited a peak in bin 11 on the offshore side along the 500-m isobath (Fig. 2B, left-hand axis). Table 1 and the cumulative histogram (Fig. 2B, right-hand axis) showed that 76% of the trajectories crossed the offshore side corresponding to bin numbers 9–13. A second peak oc-

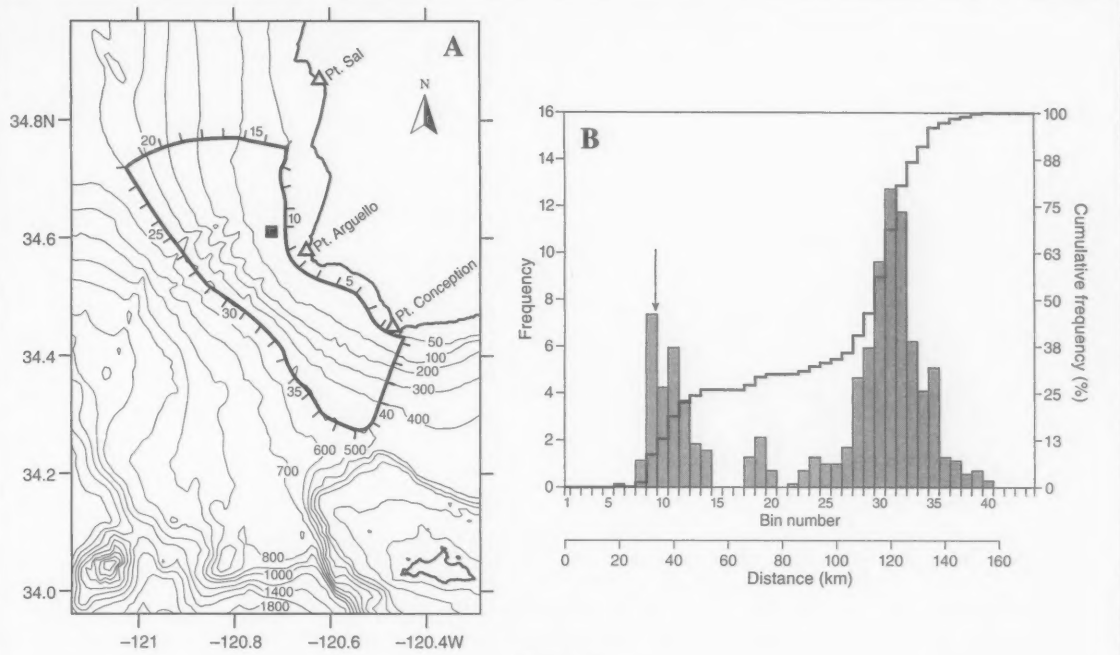

Figure 3

(**A**) Coverage boundary (indicated by heavy lines around the black square [Platform Irene]) for 1 May–31 August 2002. Numbers and tick marks around boundary identify bins corresponding to x-axis in panel B. (**B**) Histogram (gray bars, left-hand scale) and cumulative frequency (bold line, right-hand scale) show fraction of trajectories (in percent) intersecting bins around coverage boundary. Panel A shows bin locations. Distance around the coverage boundary (Fig. 2A) in kilometers is also shown (bottom scale). Arrow above histogram shows boundary location nearest Platform Irene.

Table 1

Statistics for trajectories using empirical orthogonal function (EOF) interpolation, and Scripps Institution of Oceanography drifters.

Year	Coverage boundary	Total trajectories	Trajectories intersecting coverage boundary	Trajectories intersecting inshore boundary (%) (50-m isobath)	Trajectories intersecting offshore boundary (%)	Trajectories intersecting northern boundary (%)	Trajectories intersecting southern boundary (%)	Mean residence time in coverage area (h ±1 SD)	Maximum residence time in coverage area (h)
1999	1999	590	546	10	76	9	5	19 (±12)	86
2002	2002	716	706	24	69	6	1	47 (±34)	163
2002	1999	716	712	18	66	7	8	22 (±18)	116
SIO drifters	2002	21	17	18	71	12	0	38 (±21)	79

curred in bin 3 and about 10% of trajectories crossed the inshore boundary on the 50-m isobath (bins 1–5). The remaining trajectories crossed either the northern (9%) or southern (5%) sides of the coverage boundary.

In 2002 the radars covered a substantially larger area (Fig. 3A), including about 50 km of the 50-m isobath, 70 km of the 500-m isobath along the offshore boundary, and a portion of the western entrance of the Santa Barbara Channel. The histogram of coverage boundary crossings for May–August 2002 also exhibited two peaks, one between bins 9–11 along the 50-m isobath and a second in bin 31 along the offshore side of the coverage boundary (Fig 3B). In 2002, 24% of trajectories crossed the 50-m isobath (bins 1–13), 69% crossed the

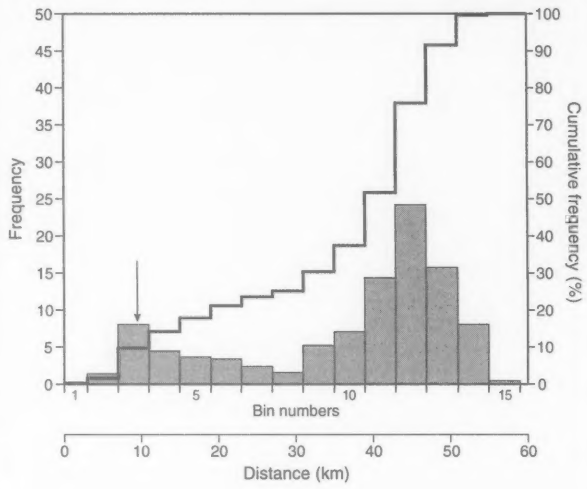

Figure 4

Histogram (gray bars, left-hand scale) and cumulative frequency (bold line, right-hand scale) showing percentage of 2002 trajectories intersecting bins from the 1999 coverage boundary. Bottom scale shows distance around the coverage boundary in kilometers. Arrow above histogram shows boundary location nearest Platform Irene.

offshore side (bins 22–39), and the remainder crossed the northern side (6%) or the southern side (1%).

To compare results more directly between years, a histogram of crossings was generated from the 2002 trajectories, using the 1999 coverage boundary. The 1999 coverage boundary was completely contained within the 2002 coverage boundary. With the 2002 trajectories, a peak in the histogram again occurred along the offshore boundary (Fig.4, left-hand scale), this time at bin 12 compared with bin 11 when the 1999 trajectories were used. A second, but much smaller peak occurred along the 50-m isobath at bin 3, consistent with the small peak along the 50-m isobath of Fig. 2B. Table 1 and the cumulative histogram (Fig. 4, right-hand scale) showed that 18% of trajectories crossed the 50-m isobath, 66% crossed the offshore side of the coverage boundary, and the remainder crossed either the northern (7%) or southern (8%) sides.

The time required for trajectories to cross the coverage boundary, defined in our study as the residence time, varied between years and mainly depended on the size of the coverage area. In 1999 the mean and standard deviation for the residence time was 19 ±12 hours, and the maximum was 86 hours (Table 1). In 2002 they were 47 ±34 hours and the maximum was 163 hours. When the 2002 trajectories were computed over the 1999 coverage boundary, residence times were comparable to the 1999 values: 22 ±18 hours and a maximum of 116 hours.

Discussion

Because of limitations in spatial coverage, the HF radar-derived trajectories could not be used to examine the full range of length and time scales over which actual trajectories may extend. We used a trajectory data set resulting from the release of Argos drifters in the region to examine these scales. Drifters were deployed in the Santa Barbara Channel and Santa Maria Basin at irregular intervals from October 1992 through December 1999 as part of a circulation study conducted by the Scripps Institution of Oceanography (SIO; see Dever [1998] and Winant et al. [2003] for a description of the drifter data set). Drifter positions were obtained up to six times per day, typically for 40 days, and had a spatial accuracy of about 1 km. Several trajectories ended earlier when the drifters beached.

No drifters were released at Platform Irene although many approached the platform after release elsewhere (130 drifters were deployed to the north of Platform Irene, and 440 were deployed to the south). To approximate trajectories originating at Platform Irene, all drifters released during all seasons for all years, and approaching within 10 km of the platform, were identified. This distance is a compromise between proximity to the platform and ensemble size; 93 trajectories approached within 10 km of Platform Irene (white circle in Fig. 5 is 10 km in radius and is centered on Platform Irene). Of these, 34 were released north and 59 south of Platform Irene. The ensemble of trajectories beginning

within 10 km of Platform Irene (gray and black dots, Fig. 5) mainly followed the trend of southward advection by the California Current System, although a smaller number extended northward from the platform and a few reached Monterey Bay. Four trajectories entered the Santa Barbara Channel.

A further sorting of the ensemble of 93 trajectories approaching within 10 km of Platform Irene to include only those during 1 May–31 August of all years produced a subset of 21 trajectories (black dots, Fig. 5). Of these, 17 crossed the 2002 coverage boundary: 3 on the 50-m isobath, 12 on the offshore boundary, 2 on the northern boundary, and 0 on the southern boundary. Although the ensemble was small, the fraction of drifters crossing the inshore boundary of the 2002 coverage area (18%) was comparable to the fraction of HF radar-derived trajectories that did so (24%), as shown in Table 1. Most trajectories crossing the offshore boundary continued offshore and southward, consistent with advection by the California Current System. Others crossing the offshore boundary extended north of Platform Irene before turning southward or offshore. The two trajectories crossing the northern boundary remained near shore and crossed the 50-m isobath north of the platform. None of these 17 trajectories entered the Santa Barbara Channel. Except for three drifters that beached, all the drifters remained offshore for the duration of Argos data logging.

Trajectories crossing the 50-m isobath tended to do so north of platform Irene, as shown by most of the computed trajectories and three of the SIO drifters (Figs. 2B and 3B). This movement indicates that transport from the platform to shallow water habitat along the mainland coast mostly occurred during times of northward, or poleward, currents. Poleward flow in the region north of Pt. Conception results from weakening or reversal of the prevailing upwelling favorable winds, the so-called "relaxation" flow state described by Dever (2004), Harms and Winant (1998), and Winant et al. (2003). They also described two other flow states, "upwelling" and "convergent," which produce offshore and equatorward transport near Platform Irene. Together these flow states have a 69% probability of occurring during May–Aug (36% for upwelling and 33% for convergent), whereas the relaxation state has a 23% probability of occurring (Winant et al. [2003], their Table 3). For comparison, 19–30% of trajectories (HF radar-derived plus actual drifters) crossed the inshore and northern boundaries, consistent with the relaxation probability and 70–81% crossed the offshore and southern boundaries, consistent with the upwelling plus convergent probability.

The trajectories can also be used to estimate recruit survival, based on the time required for transport to habitat. Recruit survival is estimated from a simple exponential decay model:

$$P(t) = P_0 e^{-mt}, \quad (3)$$

where m = mortality (0.02 or 0.06/day, Ralston[2]);

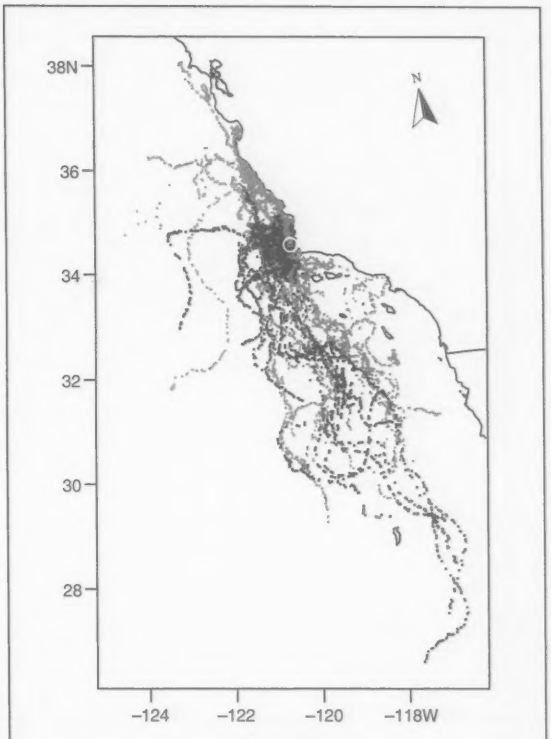

Figure 5

Trajectories of all drifters deployed by the Scripps Institution of Oceanography at various times from October 1992 through December 1999 after passing within 10 km of Platform Irene (gray dots). Also shown are all drifters after passing within 10 km of Platform Irene for only the time period 1 May–31 August for all years (black dots). White circle is centered on Platform Irene and has a radius of 10 km.

P = population at time t; and
P_0 = the initial population.

Here, P_0 represents the population of juvenile bocaccio that recruited at Platform Irene, and survival estimates are used to predict their survival in the absence of the platform. In 1999 and 2002, trajectories to habitat from Platform Irene crossed the 50-m isobath within 19–47 hours (Table 1), indicating a high percentage of survival for bocaccio (96–98%). In contrast, offshore and southward drifter trajectories from the SIO drifter data indicated much lower survival. Pelagic juvenile bocaccio transported by these flows would be carried southward by the California Current and remain far from the mainland and the Northern Channel Islands (Fig. 5)

[2] Ralston, S. 2004. Personal commun. NOAA National Marine Fisheries Service, 110 Shaffer Road, Santa Cruz, CA 95060.

for at least 40 days, the nominal time the drifters were tracked. Survival after 40 days along these trajectories ranged from 9 to 45%.

It is possible that juvenile bocaccio spend time away from near surface waters during their planktonic larval phase and therefore their trajectories may depend on deeper currents. Previous observations in the study region show strong correlation between near surface and deeper flows, indicating that inferences from surface trajectories apply to deeper trajectories. Comparing moored current meters at 5 and 45 m depth, Dever (2004), Harms and Winant (1998), and Winant et al. (2003) generally found a high correlation between current directions, and a decreased flow speed at depth. They also found that poleward flow at 45 m occurs during the convergent and relaxation states, and equatorward flow occurs during the upwelling state. Therefore, during relaxation and upwelling states, currents at 45 m likely have similar directions, but lower speeds compared with surface currents. During the convergent state, currents at 45 m are opposite surface currents, indicating that surface currents represent deeper currents only to some shallower depth.

We assumed in this trajectory analysis that juvenile bocaccio effectively behave like passive particles. We made this assumption for two reasons: 1) this assumption allowed us to focus on the lower bound of their range of possible swimming behaviors; and 2) such an assumption also eliminated the need to account for their actual swimming behavior in the open ocean, about which little is known. We do not assume that juvenile bocaccio do not swim; rather, we assume that they swim randomly such that their effective transport is similar to that of passive particles. The other behavioral limit of rapid, consistently directional swimming behavior would likely alter the fraction of bocaccio encountering shallow habitats versus the fraction being advected offshore. Flume experiments with visual cues for directional orientation demonstrate that coral reef fish in the late pelagic stage can swim up to ~100 km in 8 days (Stobutzki and Bellwood, 1997); therefore behavioral modification of trajectories could be very important. Larval and pelagic juvenile fish may possess swimming and sensory abilities to overcome passive drift in currents; however, some kind of external reference is necessary for fish to detect and respond to the direction of a current. In a review of the behavior of larval and juvenile fish in the pelagic environment, Leis and McCormick (2002) pointed out that it is yet to be demonstrated that these early-stage fish in offshore "blue water" can effectively modify current-driven trajectories by orienting to cues from settlement habitat located at a scale greater than several kilometers away. A variety of near-field stimuli, such as light and temperature gradients, sound, and visible prey affect swimming behavior. Clearly more research is needed to evaluate the effects of swimming behavior of temperate reef fishes, such as bocaccio, in order to model their dispersal. We speculate, however, that the assumption of passive dispersal will remain an important lower bound on constraining effects of swimming behavior.

Smoothing and interpolation in the processing of the HF radar velocity data limit the spatial resolution of current fluctuations to scales of ~6 km, the diameter of circles used to compute velocity vectors. Velocity structures smaller than this scale are not resolved but may be important in determining trajectories. For example, Helbig and Pepin (2002) found that errors in modeling the spatial distributions of fish eggs in an embayment increased as spatial resolution of a circulation model decreased. Assuming effects of unresolved velocity structures on smaller scales act as a diffusive process, we speculate that incorporating diffusion would cause the locations of the boundary intersections to spread to adjacent bins. In this case, peaks in the histograms (such as in Figs. 2B, 3B, and 4) would decrease as diffusion spreads boundary intersections to adjacent bins. Velocity statistics at scales of the order of a few km and smaller in our study area, however, are not available for incorporating the effects of diffusion into the trajectories. Results from actual drifters, which do contain velocity structure unresolved by the HF radars, are not very different from HF-radar-derived trajectory results (Table 1), indicating that the effects of unresolved variance are not large. For predicting settlement to habitat, trajectory improvements gained through the incorporation of smaller scale flow features may be offset by assumptions of swimming behavior and habitat location.

Questions and issues have arisen in the decommissioning process about the regional importance of platform fish assemblages (Schroeder and Love, 2004). For example, does removal of a platform impact the bocaccio population? Based on our annual research submersible surveys (detailed in Love et al., 2003) conducted in 1997, 1998, 1999, and 2001, estimates of YOY bocaccio at Platform Irene ranged from 61 (2001) to 41,000 (1999) (Lenarz[3]). YOY bocaccio abundances can be even higher than those observed at Platform Irene. We have recently estimated that, during 2003, Platform Grace, located in the Santa Barbara Channel, harbored over 300,000 YOY bocaccio (Lenarz[3]). Under even the most conservative parameters, this would translate into many thousands of adults (MacCall[4]). In addition, there is evidence that some of the bocaccio that recruit to platforms as YOYs migrate, and thus seed, natural reefs. Fish tagged at Platform A, located off Summerland, CA, in the Santa Barbara Channel, were later recovered over natural reefs over 100 km to the north and south of that platform (Hartmann, 1987). In another study, recruiting bocaccio became resident on a deep-water platform and formed the highest density of adult fish observed in the Southern California Bight

[3] Lenarz, W. 2004. Personal commun. P.O. Box 251, Kentfield, CA 94914-0251.

[4] MacCall, A. 2004. Personal commun. NOAA National Marine Fisheries Service, 110 Shaffer Road, Santa Cruz, CA 95060.

(Love et al., 2003). Thus, bocaccio that recruit as YOYs to a platform may benefit natural reefs either through emigration to these reefs or through increased larval production.

Conclusion

Observations of evolving surface current patterns obtained by HF radar are used to estimate dispersal pathways for juvenile bocaccio in the vicinity of Platform Irene, an oil production platform off the central California coast. Results indicate that most of YOY bocaccio settling around Platform Irene would not survive in the absence of the platform. Instead, prevailing currents would likely advect them offshore where they would have a very low probability of survival. Although it is possible that some individuals would encounter acceptable nursery habitat on offshore banks or islands, it is likely that most would perish. Thus, the presence of Platform Irene almost certainly increases the survival of young bocaccio in the Point Conception–Point Arguello region.

These results indicate that knowledge of regional ocean circulation patterns is essential for evaluating the effects of oil production platforms, or other artificial habitats, on dispersal pathways of juvenile fishes. Platform location, local current patterns, and natural habitat distribution determine the balance between settlement at a specific platform and settlement on natural habitat. The approach used in this study, an analysis of trajectories derived from HF radar current measurements, can provide insights into this balance. Additional research on small-scale circulations features unresolved by the radars and on swimming behavior of juvenile rockfishes will sharpen these insights.

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Behavioral ontogeny in larvae and early juveniles of the giant trevally (*Caranx ignobilis*) (Pisces: Carangidae)

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Abstract—Behavior of young (8–18 mm SL) giant trevally (*Caranx ignobilis*), a large coral-reef–associated predator, was observed in the laboratory and the ocean. Size was a better predictor of swimming speed and endurance than was age. Critical speed increased with size from 12 to 40 cm/s at 2.7 cm/s for each mm increase in size. Mean scaled critical speed was 19 body lengths/s and was not size related. Swimming speed in the ocean was 4 to 20 cm/s (about half of critical speed) and varied among areas, but within each area, it increased at 2 cm/s for each mm increase in size. Swimming endurance in the laboratory increased from 5 to 40 km at 5 km for each mm increase in size. Vertical distribution changed ontogenetically: larvae swam shallower, but more variably, and then deeper with growth. Two-thirds of individuals swam directionally with no ontogenetic increase in orientation precision. Larvae swam offshore off open coasts, but not in a bay. *In situ* observations of *C. ignobilis* feeding, interacting with pelagic animals, and reacting to reefs are reported.

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The giant trevally (known as ulua aukea in Hawaii) (*Caranx ignobilis* (Forsskål)), is the largest species in the commercially important family Carangidae. It has a wide tropical Indo-Pacific distribution ranging from Japan to Australia and from East Africa to the Hawaiian and Marquesas Islands (Randall et al., 1997; Smith-Vaniz, 1999; Hoese et al., in press). Adults of this reef-associated pelagic species may be solitary or form schools on inner reefs, inshore on sand flats, or in reef channels, but primarily on seaward reefs to depths of 80 m (Kuiter, 1993; Myers, 1999; Hoese et al., in press). *Caranx ignobilis* is an important top-level carnivore in reef systems: adults and juveniles feed during the day primarily on demersal and pelagic fishes and to a lesser extent on cephalopods and crustaceans (Blaber et al., 1983; Sudekum et al., 1991; Myers, 1999). Adult coloration varies from silver grey to almost black above and fins are usually dark grey to black, but in small juveniles the body is barred (pale to dark gray) and the anal and caudal fins are yellow (Kuiter, 1993; Randall et al., 1997). *Caranx ignobilis* is important to commercial and recreational fisheries and to aquaculture because of its size (maximum of 1.7 m and 62 kg), abundance, palatability, and reputation as an excellent game fish (Smith-Vaniz, 1999; Yu, 2002). The species can, however, be ciguatoxic (Myers, 1999).

Little is known of the early life history of *C. ignobilis*. Adults, which reach maturity at about 60 cm in length and 3–4 years of age, have been reported to gather on shallow seaward reefs and offshore banks to spawn (von Westernhagen, 1974; Johannes, 1981; Sudekum et al., 1991; Myers, 1999). Neither eggs nor larvae have been described, and nothing is known of the distribution or behavior of the larvae or early juveniles. Juveniles are found in small schools over sandy inshore bottoms (Myers, 1999), but also in turbid estuaries, where they are "uncommon" (Blaber et al., 1983). Juveniles and subadults have wide tolerances for salinity and turbidity (Blaber et al., 1983). In Kaneohe Bay, Hawaii (a coral-reef lagoon with estuarine features), *C. ignobilis* juveniles less than 20 cm (<1 year old) were found on the "murky" lagoon floor (Wetherbee et al., 2004). Juveniles were associated with lagoonal patch reefs when they were between 25 and 40 cm in length, and appar-

ently moved out of the bay when larger than 40 cm. In South African estuaries, individuals larger than 55 cm were absent (Blaber et al., 1983). The high abundance of *C. ignobilis* in the NW islands of Hawaii (Sudekum et al., 1991), where estuaries are absent, shows that presence of juveniles in estuaries is facultative.

Recently, Taiwanese aquaculturists have developed culture methods for *C. ignobilis* (Yu, 2002), and this enabled us to obtain larvae and small juveniles that we used for laboratory and field observations of behavior. Behavior of early-life history stages of marine fishes can strongly influence both the survival and distribution of these small fishes (Leis and McCormick, 2002). Therefore, an understanding of the behavioral capabilities of these early-life history stages is essential to intelligent management, and to comprehend the demographics and ecology of any marine teleost fish.

Aside from field studies of the behavior of wild larvae in vertical distribution (e.g., Ahlstrom, 1959; Olivar and Sabatés, 1997; Flores-Coto, et al., 2001), behavior has been studied in the early-life history stages of only a few carangid fishes. There has been extensive research on cannibalism, aggressive interactions, and schooling behaviour by using reared larvae and juveniles of Japanese amberjack (*Seriola quinqueradiata*) and white trevally (*Pseudocaranx dentex*) in the laboratory (e.g., Masuda and Tsukamoto 1996, 1998, 1999; Sakakura and Tsukamoto 1996, 1999). We report in the present study the first observations of the development of swimming abilities, orientation abilities, and vertical distribution for *C. ignobilis,* using both *in situ* methods (Leis et al., 1996) and laboratory swimming chambers (Fisher et al., 2000). These behaviors are important to dispersal, feeding, predator interactions, and survival generally during the early life history of *C. ignobilis*.

Materials and methods

Larvae and juveniles

Young *C. ignobilis* were obtained from a commercial aquaculture farm near Kaohsiung, Taiwan. They were identified as *C. ignobilis* by the farmer with reference to photographs, and the identification was subsequently confirmed by examination of preserved specimens. *Caranx ignobilis* eggs from an induced spawn were placed in a large outdoor earth pond (approximately 20×20×1m), and thus hatched under "natural" conditions. Larvae were provided with a "natural" food source (phytoplankton and zooplankton that were resident in the pond). Surface water temperature in the outdoor pond was 32°C when the larvae were collected in May 2004. Fish were obtained on two occasions at the same pond from a single cohort and from an unknown number of females; the first collection was at 20 days after hatching (dah) and the second at 24 dah.

The young fish were placed in oxygenated plastic bags in an insulated box and transported to the laboratory at the National Museum of Marine Biology and Aquarium (NMMBA), Kenting, Taiwan, about 1 hour by road. In the laboratory the larvae were acclimated in a 40-liter aquarium filled with water from the seawater system at NMMBA. Each aquarium was fitted with an aerator, and kept ca 25°C. Twice daily, the larvae were fed with live, newly hatched brine shrimp (*Artemia*) nauplii and 50% of the total volume of water exchanged with fresh seawater. The aquaria were cleaned daily by suctioning debris off the bottom.

Reported sizes of larvae are given in standard length (SL, in mm). Ages are reported as days after hatching (dah) and are based on the age reported by the aquaculturist when the larvae were obtained. The nomenclature for early life history stages of fishes is complex; there are many different systems of terminology and no consensus on which is the most appropriate. Depending on the nomenclature used, the *C. ignobilis* individuals we studied (Fig. 1) would be considered larvae, or juveniles, or as a mixture of both. In our *C. ignobilis*, all fin-rays were present in the smallest specimens (8 mm), and scales were present from about 14 mm, yet the preopercular spines that characterizes most carangid larvae (Leis and Carson-Ewart, 2004) were still present at 19 mm. Unlike the pelagic stages of demersal fishes, *C. ignobilis* does not undergo a clear ecological transition from pelagic to demersal habitat upon which one might base life history stages. We do not attempt to distinguish between larvae and juveniles, and to avoid awkward phrasing and for simplicity, we refer to the young fish that we studied as larvae on the basis that the largest individuals retained some head spines. We acknowledge that in some taxonomic systems they may be referred by other terms.

Laboratory observations

Multilane swimming chambers were used to measure swimming abilities (Stobutzki and Bellwood, 1994). One chamber was used to measure critical speed and a second identical chamber was used for measurements of endurance (Fisher et al., 2000). Both chambers were made of clear plexiglass and had 6 lane-ways, each 30 mm wide, 50 mm high, and 180 mm long. A black line across the lid of the chamber provided the larvae with a point of reference for orientation. Aside from the fine mesh (0.5-mm) ends, the chamber design was identical to that of Stobutzki and Bellwood (1994, 1997).

Even distribution of flow was achieved by a T-piece diffuser in the header portion of the chamber. Turbulence in the chamber was minimized by a 40-mm-long section of flow straighteners at the start of each lane. These straighteners also minimized possible boundary layers. Previous measurements have shown that water velocity in the 5 mm area closest to the wall was not significantly different from that in the center of the chamber (Stobutzki and Bellwood, 1997; Stobutzki, 1998; Fisher et al., 2000). Water flow speed was controlled by turning a calibrated ball valve. Flow rates were calibrated by recording the time taken for water

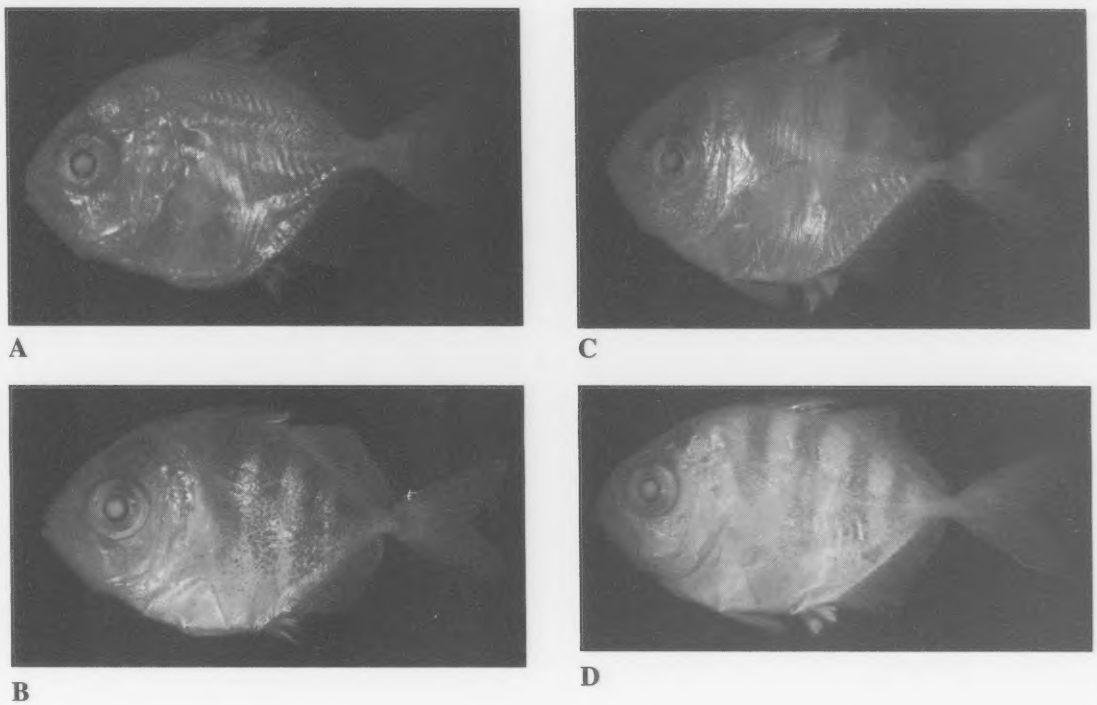

Figure 1

Preserved larvae of giant trevally (*Caranx ignobilis*) representing the range of sizes and developmental stages included in the present study. Preopercular spination was present in all specimens. The smallest specimen had a few scutes on the peduncle, the 14.5-mm specimen had scales forming elsewhere, and the largest specimen was largely scaled. Sizes are SL (Australian Museum catalogue numbers are provided). (**A**) 9.6 mm (I.43435-004); (**B**) 11.7 mm (I.43435-003); (**C**) 14.5 mm (I. 43435-004); (**D**) 18.5 mm (I.43435-002).

flowing over the outlet weir to fill a container of known volume, divided by the cross-sectional area of the chamber. The average of five calibrations was used as the flow speed for a given valve angle. The chambers were calibrated each time they were set up. Flow speeds in excess of 50 cm/s could be achieved with this system. The chambers were plumbed into the seawater system of the NMMBA aquaria and laboratory, which provided a continual flow of "fresh" seawater.

Before measurements of swimming speed and endurance were recorded, the larvae were acclimated to any differences in water quality between the holding tank and swimming chamber by gradual addition of seawater from the swimming chamber system. Larvae were placed in a chamber lane and allowed to acclimate for 5 minutes at 1 cm/s. Any larva showing signs of stress during the acclimation period was removed from the experiment and replaced with another individual. Water temperature in the swimming chamber ranged from 27° to 29°C. Two swimming parameters were measured: critical speed (U_{crit}), which measures maximum swimming speed over periods of minutes, and endurance, which measures how long larvae can swim without food or rest.

For U_{crit} tests, starting at 1.5 cm/s flow speed was increased by approximately 2 cm/s every 5 minutes until the larvae were unable to swim against the flow. The elapsed time when each larva drifted to the downstream mesh was recorded. Critical speed (U_{crit}) of larvae was calculated with the equation of Brett (1964):

$$U_{crit} = U + (t/t_i \times U_i),$$

where U = penultimate speed;
U_i = speed increment (ca. 2 cm/s in the present study);
t = time swum in the final speed increment; and
t_i = the time interval for each velocity increment (5 min).

The total time for a critical speed measurement was proportional to the U_{crit} achieved, and varied from 15

Table 1

Location-specific relationships between *in situ* speed (cm/s) and size (mm SL) in *Caranx ignobilis* larvae. NA=not applicable.

Location	*n*	Regression	r^2	*P*
Wan Li Tong	7	$Spd = 1.69SL - 6.2$	0.83	<0.002
Her Chen	3	$Spd = 2.55SL - 12.2$	0.97	0.11
Nan Wan Bay South	2	$Spd = 0.12SL + 4.9$	NA	NA
Nan Wan Bay North	6	$Spd = 2.05SL - 17.9$	0.72	0.03

minutes for the slowest individual to 82 minutes for the fastest. Given the endurance of which these larvae are capable (see "Results" section), it is unlikely that the larvae would have become fatigued over such time intervals.

For endurance tests, a constant speed of 10 cm/s was used. Larvae were swum until they fatigued, which was defined as the time when a larva could no longer hold its position against the current and drifted onto the downstream mesh. During daylight hours, larvae were observed regularly and the exact time of fatigue (=swimming duration) was recorded. If a larva fatigued when it was not being observed, the time at fatigue was estimated as the midpoint between the time when the larva was last seen swimming and the time when it was found no longer swimming. Chambers were set up under cover so that they were shaded throughout the day, and a fluorescent light was used for illumination at night. The actual endurance measurements of time swum were converted to distance swum, by using the flow speed data, and were reported as kilometres swum.

Fatigued larvae from both experiments were removed from the chamber, euthanized and fixed in Bouin's solution for one hour, then placed in 70% alcohol and stored. All preserved larvae were later examined under a dissection microscope to determine standard length (SL) and state of notochord flexion. Total lateral area (TA) and propulsive area (PA) of larvae (Fisher et al., 2000) were measured by using Scion Image for Windows (Beta 4.02, Scion Corporation, Frederick, MD). PA is TA minus the head and gut.

In situ observations

Four sites were used for *in situ* observations of *C. ignobilis* in the South China Sea, at the southern tip of Taiwan (ca. 22°N, 121°E). Two study sites were used in Nan Wan Bay (21 May 2004) where the depth range was 14–23 m and another two were used on the west coast just off the peninsula that delineates the west side of Nan Wan Bay in the vicinity of Wan Li Tong and Her Chen (14 May 2004) at a depth range of 17–31 m (Table 1). At each site, observations were made at least 50 m offshore, and all observations were conducted in the morning.

Larvae were transported from the laboratory to the release sites in covered buckets fitted with a battery-operated aerator. Ambient seawater was gradually added to the buckets to allow the larvae to acclimatize to the surrounding water conditions. Then, 50% of the water in the bucket was exchanged for "fresh" seawater every hour. The behavior of the larvae was observed following the procedures of Leis et al. (1996) and Leis and Carson-Ewart (1997, 1998). Two scuba divers descended to a depth of 5 m where the observer diver released a larva from a small container. Once the larva chose its initial trajectory, the two divers followed. The observer diver's sole job was to follow the larva while the second diver, following the observer, recorded data. The direction the observer diver was facing when he or she released the larva was chosen at random. Each larva was used only once and, where possible, was recaptured at the end of the observation period and preserved. The size of each larva was estimated, with the aid of a ruler, before release. For recaptured larvae, the estimated and actual sizes were regressed, and this relationship was used to calculate the actual size of the five individuals that were not recaptured of the 24 released. Water column depth was measured by the depth sounder on the support boat at the start of each larval release.

Swimming speed, depth, and swimming direction were measured *in situ*. We attempted to observe each larva for 10 minutes, taking measurements of swimming direction and depth, using a dive compass and computer, respectively, every 30 seconds. Speed was calculated from distance traveled as measured by a calibrated flowmeter over the full period of observation (Leis and Carson-Ewart, 1997). Larvae were not followed deeper than 15–18 m on some dives for safety reasons; therefore observations on some individuals were curtailed. Twenty-four larvae were observed, and observations on 18 of the larvae lasted the full 10 minutes. Five larvae swam monotonically downward to below our safety depth from 3 to 6 minutes, whereas one initially ascended, before descending after 5 minutes and exceeding the safety depth after 8 minutes.

Data analysis

To determine the best predictor of performance, values of critical swimming speed and endurance were regressed against SL, TA, and PA by using linear, logarithmic, power, and exponential models. The model with the greatest r^2 (coefficient of determination) was used as the best description.

All bearings are given as degrees magnetic. Cardinal directions are not abbreviated, but other directions are abbreviated (e.g., SE for southeast). From these bearings and the flowmeter data, we estimated swimming direction and speed in relation to the water (not the bottom).

Circular statistical procedures followed Batschelet (1981) and Zar (1996). Mean vector length (r), is a measure of angular dispersion ranging from 0 (maximum dispersion) to 1 (lack of dispersion). The Rayleigh test was used for single-sample hypotheses about directional swimming. Watson-Williams test was used for hypotheses about directional swimming involving more than one sample. Most of the circular statistical procedures were performed with Oriana software (vers. 2, Kovach Computing Services, Pentraeth, Wales, UK). For all statistical tests, we report actual P values whenever possible, but consider $P<0.05$ to constitute a "significant" result.

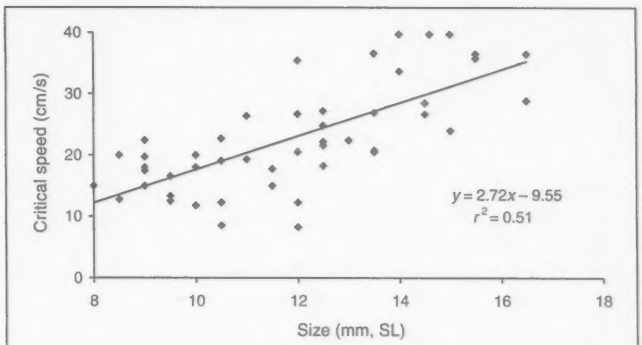

Figure 2

Critical speed of giant trevally (*Caranx ignobilis*) larvae of different sizes. At any size, variation in swimming speed was large.

Results

Larvae used in the critical speed trials were 21–30 days old, and ranged from 8.0 to 16.5 mm SL. Larvae up to 18 mm were used in the *in situ* observations. All fins were formed in the smallest individual and over the size range studied, the larvae were very deep bodied, primarily silver, and usually had six dark vertical bars laterally. Although the specimens used on any day did not constitute a random sample of the available sizes, they could be used to obtain a rough estimate of the growth rate over the experimental period. The range of size-at-age on any day was as much as 6.5 mm. Average growth over this period was 0.36 mm/d, and the slope of the size versus age line was significantly different from zero, but the relationship between size and age was weak (size=0.36 age + 2.87, $P<0.001$, $r^2=0.28$). Total lateral area increased approximately as the square of SL ($TA=0.51SL^{2.01}$, $r^2=0.93$), whereas propulsive area increased at a lower rate ($PA=0.34SL^{1.96}$, $r^2=0.94$).

Critical speed

Critical speed was measured in 54 individuals in eight batches of six over 10 days. Critical speed increased with size from about 12 cm/s in the smallest individuals (ca. 8 mm) to about 40 cm/s in the largest (16.5 mm, Fig. 2). For SL, a linear model provided the best fit for this relationship ($U_{crit}= 2.72SL–9.55$, $P<0.001$, $r^2=0.51$, $n=54$), but the difference between the linear model and the others was small (r^2 for the other models ranged from 0.43 to 0.49). Both TA and PA gave somewhat better fits than SL ($U_{crit}= 0.39TA + 5.25$, $r^2=0.58$; $U_{crit}= 0.22PA +5.73$, $r^2=0.55$). Size was a much better predictor of critical speed than was age ($U_{crit}=0.90age–0.22$, $P<0.01$, $r^2=0.13$, $n=54$).

The fastest individual within each 1-mm increment of size was considered the best performer, and these constituted 16.6% of all larvae. These nine best performing larvae swam at 20 to 40 cm/s. The nine best performing larvae had the same increase in performance with size (2.7 cm/s per each mm of growth) as the "all-individuals" line, but were 8 cm/s faster at all sizes ($U_{crit}=2.69SL–1.46$, $P<0.001$, $r^2=0.76$). Therefore, both average performers and "best performers" increased speed at 2.7 cm/s per each mm of growh in SL.

Scaled speed in terms of body lengths per second did not increase significantly with size ($P=0.07$, $r^2=0.06$), and the overall mean (±standard error) was 19 ±0.7 BL/s. The fastest 10% of individuals swam at a mean U_{crit} of 28.2 ±0.6 BL/s.

In situ speed

In situ speed was measured in 24 individuals ranging in size from 8.5 to 18 mm SL. Some individuals stopped and hovered at times during the observation period, but these pauses in swimming were incorporated into the speeds measured over the observation period. Observations were made a week apart when the larvae were 24 and 31 days old, respectively, and at a total of four locations that differed in depth, exposure, and bottom type. Observed *in situ* speeds ranged from 3 to 19 cm/s. The *in situ* speeds were less than the critical speed measurements (see below). Mean scaled *in situ* speed was 9.5 ±0.9 BL/s.

Overall, there was no significant increase in speed with size ($P=0.89$, $r^2=0.001$, $n=24$), but it was obvious that the larvae behaved differently in the different locations; therefore we examined the data for each location separately. Further, we eliminated observations on one larva that simply drifted without swimming and on four individuals that quickly swam to depths greater than 18 m and thus provided less than 5 minutes of observations, because short measurements of speed taken at steep angles of descent can be inaccurate. The *in situ* speed data on the 19 remaining individuals were used.

For each location, *in situ* speed increased with size, as expected, except, perhaps for the largest individual (Table 1, Fig. 3). For the three locations with three or more observations, *in situ* speed increased at 1.7–2.6 cm/s per each mm of growth depending on location (Table 1), and the 95% confidence interval for the three slopes overlapped broadly. However, because the height of the speed versus size lines varied (*y* intercept ranged from −6 to −18), the actual speed at any size differed among locations by as much as 10 cm/s. For the *in situ* speed data, PA provided fits with r^2 values that were very similar to those of SL. The r^2 for PA was 0.07 higher than that for SL for Nan Wan Bay North, equal for Her Chen, and 0.15 lower for Wan Li Tong.

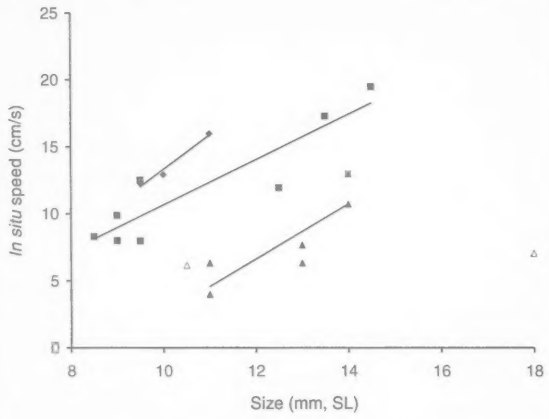

Figure 3

In situ speeds of giant trevally (*Caranx ignobilis*) larvae and juveniles of different sizes at different locations. Locations of observations were ■ Wan Li Tong, 14 May 2004; ♦ Her Chen, 14 May 2004; ▲ Nan Wan Bay North, 24 May 2004; ▲ Nan Wan Bay South, 24 May 2004. See Table 1 for details of best-fitted regression lines for each area. No line was fitted to the two points from Nan Wan Bay South.

Table 2

Comparison of two measures of size-specific speed (cm/s) in *Caranx ignobilis* larvae. Dashes indicate that no data were available.

Size interval (mm, SL)	Mean *in situ* speed (*n*)	Mean U_{crit} (*n*)	Ratio: *in situ*/U_{crit}
8.1–9.0	8.7 (3)	17.5 (3)	0.50
9.1–10.0	11.4 (4)	15.3 (12)	0.75
10.1–11.0	8.1 (4)	18.0 (6)	0.45
11.1–12.0	– (0)	20.2 (9)	—
12.1–13.0	8.6 (3)	24.5 (9)	0.35
13.1–14.0	13.7 (3)	30.7 (7)	0.45
14.1–15.0	19.5 (1)	29.7 (4)	0.66
15.1–16.0	– (0)	36.1 (2)	—
16.1–17.0	– (0)	32.7 (2)	—
17.1–18.0	7.0(1)	– (0)	—
Mean ±SE			0.52 ±0.15

Comparison between critical speed and *in situ* speed

For each 1-mm (SL) increment in size, we calculated a mean speed for both critical speed (54 individuals) and *in situ* speed (19 individuals). These size-specific speeds are summarized in Table 2 (both measurements were not available for every size increment). The ratio of the two size-specific measures (*in situ*/U_{crit}) ranged from 0.35 to 0.75, and had a mean value of 0.52 ±0.15. The size-specific speed measures were not significantly correlated (*in situ*=0.45U_{crit}+1.45, r^2=0.47, P=0.13, n=6). Scaled *in situ* speed (BL/s) was one-half scaled U_{crit}.

Endurance

Endurance data were available for 12 individuals ranging in size from 9 to 14 mm SL, and for two ages (21 and 24 days at the start of the endurance run) measured in two batches of six. The range in fish swimming times was 12.6 to 105 hours. Swimming endurance increased with size from about 5 km in the smallest individuals to about 40 km in the largest (Fig. 4). Again, a linear model provided the best fit for this relationship (*End.*=5.2*SL*−41.5, P<0.001, r^2=0.80, n=12), and the difference between the linear model and the others was small (r^2 for the other models ranged from 0.73 to 0.79). In contrast to critical speed, the fit of the relationship between size and performance was not improved by using TA or PA instead of SL (r^2=0.57 and 0.62, respectively). Endurance also increased with age, but endurance data were available only for larvae of two ages (21 and 24 days). Size was a better predictor of performance than was age (*End.*= 6.6*age*−128, P=0.001, r^2=0.66, n=12).

Vertical distribution

There was not a significant overall relationship between mean swimming depth and size (P=0.29, r^2=0.05). In spite of this, larvae of different sizes differed in their depth selection behavior. The smallest larvae (8–10 and 10–12 mm) swam primarily between 4 and 10–12 m (Fig. 5, A and B). One larva of each of these smallest size groups did, however, swim deep monotonically. If one ignore these two deep-swimming larvae, both smallest size groups reached an overall mean depth of about 9 m

at about 5 minutes. The smaller (8–10 mm) larvae then stayed at about 9 m, whereas the larger (10–12 mm) larvae gradually ascended, reaching a mean depth of about 6 m by the end of the 10-min observation period. In contrast, larvae of 12–14 mm were more varied in their depth ranges, some reaching the surface, whereas others remained within 2–3 m of the release depth (Fig. 5C). Larvae of 12–14 mm had no overall temporal trend in depth and maintained a mean depth of about 5–6 m throughout the study period. Several of the larvae of this group did oscillate over a depth range of several m during the 10-min observation period. The largest larvae (14–18 mm) had more varied vertical-distribution ranges, leading to high amplitudes (Fig. 5D). Three of the five largest larvae swam deep monotonically and the other two oscillated—one reaching the surface after an initial descent, whereas the other reached our lower dive limit (16 m), but only after first ascending above the release depth for the first 5 minutes.

We found a weak relationship between depth amplitude (difference between deepest and shallowest observations) and size ($amp.=0.44SL + 1.7$, $P=0.03$, $r^2=0.21$, $n=24$); larger individuals swam over a greater range of depths owing to the tendency of larger larvae to either oscillate or to swim deep monotonically. Water column depth did not influence either mean swimming depth ($P=0.11$, $r^2=0.11$) or amplitude ($P=0.06$, $r^2=0.15$).

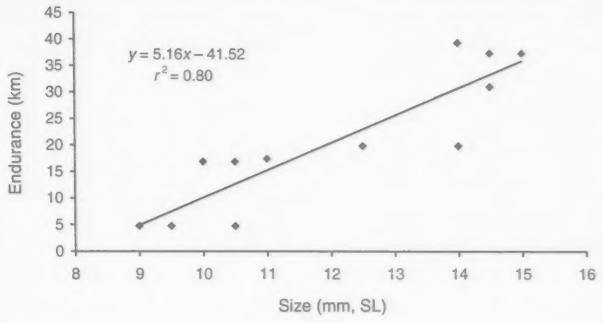

Figure 4

Endurance swimming of giant trevally (*Caranx ignobilis*) larvae of different sizes.

Table 3

Directionality of *in situ* swimming for *Caranx ignobilis* of different sizes. Only values from directional individuals are included for r (the length of the mean vector, which ranges from 0 to 1): the higher r, the more directional was the trajectory.

Size interval (mm SL)	*n*	*n* directional (Rayleigh test, $P<0.05$)	Range of r	Mean r
8–10	8	6	0.41–0.86	0.73
10–12	5	2	0.60–0.90	0.75
12–14	6	4	0.60–0.83	0.72
14–18	5	4	0.45–0.92	0.74

Orientation

Sixteen of the 24 larvae observed *in situ* had directional trajectories ($P<0.05$, Rayleigh test, Table 3). Figure 6 represents the direction frequency distribution of a *C. ignobilis* larva with average directionality. The remaining analyses included only the 16 individuals for which directional trajectories were found (termed "directional larvae" or "directional individuals" for the sake of brevity), but the same result was obtained when all 24 individuals were included. If all locations were considered together, the mean swimming directions of these 16 individuals had no overall directionality ($P>0.20$, Rayleigh test). In contrast, there was significant overall directionality off the west coast (Fig. 7A) where the larvae swam, on average, offshore or toward the west (269°, Rayleigh test, $P=0.024$). There was no indication of any overall directionality in mean swimming direction in Nan Wan Bay (Fig. 7B) (mean direction, 145°, $P=0.58$, Rayleigh test). Overall swimming direction, however, differed significantly between the west coast and Nan Wan Bay (Watson-Williams test, $P=0.028$).

We found only a limited indication that the directionality of the larvae changed with size (Table 3). There was no ontogenetic increase in precision of directionality (measured as r, the length of the mean vector) ($r^2=0.05$, $P>0.10$). Similarly, although the mean size of the eight nondirectional larvae was 11.6 mm, and that of the 16 directional larvae was 12.2 mm, this difference was not significant (*t*-test, $P=0.22$). In terms of overall orientation, larvae observed off the west coast were smaller by about 4 mm (*t*-test, $P=0.002$) and were studied a week earlier than those studied in Nan Wan Bay; therefore it is possible that the difference in overall swimming direction between locations was due to temporal or ontogenetic factors rather than to spatial factors. At the west coast location, the overall mean direction of the five small (8–9.5 mm) directional larvae was the same (268°) as the overall mean direction of the 4 large (10–14.5 mm) directional larvae, indicating there was no ontogenetic change in directionality.

Finally, within trajectories, there was no increase in directionality with time. The r value for the first half of the trajectories was not significantly different from the r value for the second half of the trajectory (Wilcoxon signed-rank test, $P>0.2$). Nor was there any indication that larger larvae had a greater difference in r between the first and second halves of their trajectories than did smaller larvae ($r^2=0.02$, $P>>0.20$).

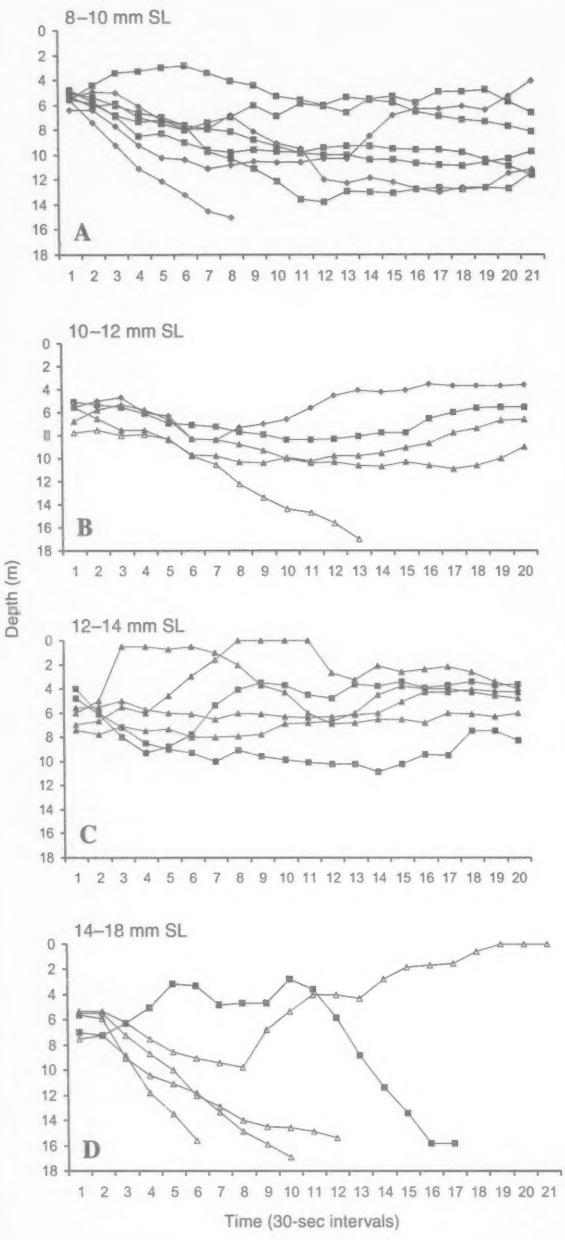

Figure 5

In situ vertical distribution trajectories for giant trevally (*Caranx ignobilis*) larvae and juveniles of four size groups. Locations of observations were ■ Wan Li Tong, 14 May 2004; ♦ Her Chen, 14 May 2004; ▲ Nan Wan Bay North, 24 May 2004; ▲ Nan Wan Bay South, 24 May 2004. (**A**) 8–10 mm SL larvae; (**B**) 10–12 mm SL larvae; (**C**)12–14 mm SL larvae; (**D**) 14–18 mm SL larvae.

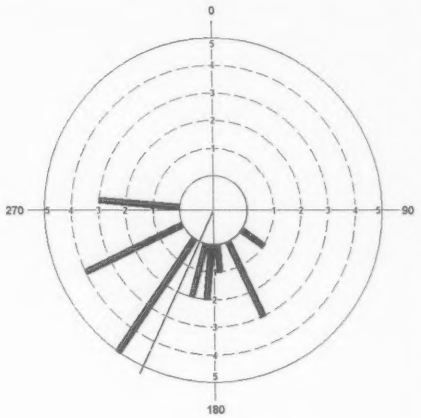

Figure 6

Frequency distribution of *in situ* swimming directions based on bearings taken every 30 seconds for an 18-mm-SL giant trevally (*Caranx ignobilis*,) at Nan Wan Bay South. Bearings are grouped into 10° intervals. The radius that penetrates the outer circle (thin line) is the mean direction. This significantly directional distribution (Rayleigh test, P=0.000001) has an r (length of the mean vector) of 0.76, which is close to the overall mean for the 16 directional individuals (Table 3). The numbers on dashed lines represent the number of times that bearing was recorded for a larva.

Other behaviors

Unplanned observations were made of feeding, interactions with other pelagic animals, and reactions with the bottom. At least nine of the 24 larvae were seen feeding, grabbing at, and apparently eating small zooplankton while swimming. One 12-mm larva encountered a large (ca. 30–40 cm) *Naso* sp. in open water and changed direction by 140° over the following minute. An 11-mm *C. ignobilis* encountered a jellyfish and briefly (<30 s) hovered under it. Five individuals (9–13.5 mm SL) came into visual contact with relatively high-relief coral reefs (at least the divers could clearly see the reefs) at Wan Li Tong and Her Chen. The larvae showed no particular interest in the reefs; two ascended slightly (0.5–1 m), two maintained a distance of 3–4 m from the reef surface as they swam over it, and one turned offshore. One 12.5-mm larva passed through a strong thermocline at 8 m that was very noticeable to the divers without slowing or giving any indication that the temperature change was sensed.

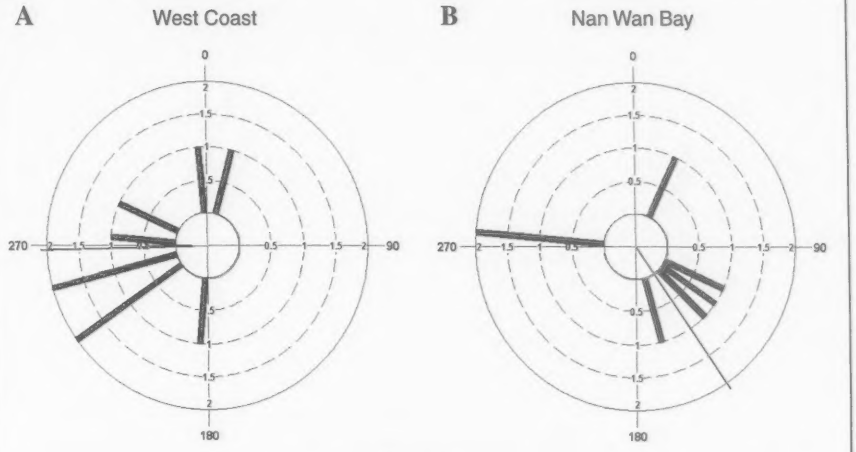

Figure 7

Frequency distributions of mean *in situ* swimming directions for giant trevally (*Caranx ignobilis*) larvae at two locations. Thick lines represent mean values for individuals, and the radius (thin line) that penetrates the outer circle represents the overall mean. The numbers on dashed lines represent the number of times that bearing was recorded for a larva. (**A**) West coast off Wan Li Tong and Her Chen, where larvae swam offshore: overall mean=268°, r=0.59, P=0.04. (**B**) Nan Wan Bay, where larvae had no overall swimming direction: overall mean=146°, r=0.29, P=0.58. "r" is the length of the mean vector, P is for the Rayleigh test.

Discussion

Previous studies of the behavior of larval carangids have focused primarily on their vertical distribution in the ocean and have been based on plankton net samples and on observations of the development of schooling-related behavior in the laboratory (see references at the beginning of this article). There have been no previous studies on the ontogeny of orientation or of vertical distribution determined from *in situ* observations, and only one article has considered the development of swimming abilities of carangid larvae.

Growth rates in *C. ignobilis* larvae of 0.36 mm/d in the laboratory and ca. 0.3–0.8 mm/d at the aquaculture farm at Kaohsiung, where we obtained larvae for our experiment, were comparable to the few reported field growth rates for larvae of other carangids. Small (<5 mm SL) larvae of Atlantic bumper (*Chloroscombrus chrysurus*) grew at 0.3–0.4 mm/d in the Gulf of Mexico (Leffler and Shaw, 1992), and larvae of two species of *Trachurus* grew at 0.2–0.7 mm/d (Hewett et al., 1985; Jordan, 1994). The *C. chrysurus* larvae were found at 26–30°C, whereas the two *Trachurus* spp. were living at about 15°C. In *T. declivis* (greenback horse mackerel), 8-mm larvae were about 17 days old and 12-mm larvae were about 22 days old (Jordan, 1994). In *T. symmetricus* (Pacific jack mackerel), a 10-mm larva was 40 days old and a 20-mm larva was about 57 days old (Hewitt, 1981). Growth rates for *C. ignobilis* in culture or in the laboratory are unlikely to be relevant to field situations, and the available field measurements of other species are either for much smaller larvae or for individuals in much cooler water and are unlikely to be applicable to *C. ignobilis*. Therefore, it is not possible to relate the size-based performance measures reported in our study to ages of larvae in the field. Further, for the laboratory-reared larvae that we used, size was a much better predictor of performance than was age, as is generally found to be the case (e.g., Fuiman and Higgs, 1997; Clark et al., 2005). We found that using PA instead of SL as a measure of size resulted in little or no improvement in the proportion of the variation in swimming performance that was explained by the linear relationships developed in our study. Other studies have had mixed results in this regard (Fisher et al., 2000; Clark et al., 2005).

Swimming speed of *C. ignobilis* increased rapidly with growth for both critical speed and *in situ* speed, although the rate of increase was greater for critical speed. Both in terms of actual speeds and rate of increase with growth, critical speeds of *C. ignobilis* are within the range of reported values for larvae of other warm water marine perciform fishes (Fisher et al., 2000; Clark et al., 2005). For larvae of benthic fishes about to settle (ca. 8–12 mm SL), pomacentrids have higher U_{crit} values than *C. ignobilis*, whereas apogonids, percichthyids, sciaenids, and sparids have similar U_{crit} values. *Seriola quinqueradiata* is the only other caran-

gid for which we could find information on ontogeny of swimming abilities (Sakakura and Tsukamoto, 1999), although the method of measuring swimming performance (so-called "routine speed") differed from those used in our study. Reared *S. quinqueradiata* larvae and juveniles of 5–40 mm TL were filmed swimming in small (30-cm diameter, 7-cm deep) laboratory tanks lacking currents and the speed was measured over 3-min intervals. Speed of *S. quinqueradiata* increased at about 0.4 cm/s per each mm of growth until about 10 mm TL, after which speed remained steady at about 2–2.5 cm/s. This is much slower, both in terms of rate of increase and absolute speed, than was found for either measure of swimming speed in *C. ignobilis*. Possibly, the slow speeds for *S. quinqueradiata* were due to the small containers in which the fish were confined and which lacked currents, as has been found for other species (Theilacker and Dorsey, 1980).

Although we did not study larvae smaller than 8 mm SL, it is safe to assume that smaller larvae have poorer swimming abilities. Previous investigations of swimming ontogeny have revealed that critical speed increases steadily with size (Fisher et al., 2000; Clark et al., 2005), as we did in our study; therefore it seems likely that a reasonable estimate of performance of smaller larvae can be obtained by extrapolating the linear relationship in Figure 2. Thus, a larva of 5 mm (about the size when the caudal fin is formed in carangids; Leis and Carson-Ewart, 2004) would be expected to have critical speeds of about 4–5 cm/s. We found that critical speeds for *C. ignobilis* were about twice *in situ* speeds, and similar relationships have been found for larvae of other species at other sizes (Fisher and Wilson, 2004; Leis and Fisher, in press). Therefore, a 5-mm *C. ignobilis* would be expected to be able to swim at about 2 cm/s (=72 m/h) in the ocean. This speed would have limited effectiveness for directly influencing horizontal position, but would be sufficient to determine vertical distribution at scales over which fish larvae are known to migrate vertically.

To put these swimming performances into an ecological context requires knowledge of ambient currents in the area of interest. If it is assumed that effective swimmers (those with swimming speed equal to or greater than average current speed [Leis and Stobutzki, 1999]) have the ability to control their dispersal by horizontal swimming, then the size at which larvae become effective swimmers is of interest to dispersal modelers. For example, at Lizard Island on the Great Barrier Reef, average current speeds are 10–15 cm/s (Frith et al., 1986). At Lizard Island, average performing *C. ignobilis* would become effective swimmers at about 7–9 mm SL on the basis of critical speed, and at about 11–14 mm based on *in situ* speed which is about half of critical speed (assuming the relationship between *in situ* and critical speeds found in the present study). The best performers would be able to reach these mean Lizard Island current speeds at about 4–6 mm SL, if based on critical speed (assuming the relationship in Fig. 2 applies to smaller larvae), and at 8–12 mm if based on *in situ* speed. Larvae that are too small to be effective swimmers may still readily influence their dispersal by other means, particularly by vertical swimming where current velocity is not uniform with depth (Sponaugle et al., 2002; Paris and Cowen, 2004). Speeds of only 1 cm/s (36 m/h) are sufficient for vertical migration, and this could be achieved by very small larvae. Indeed, vertical movements by small carangid larvae are well documented in studies where plankton nets were used (e.g., Ahlstrom, 1959; Olivar and Sabatés, 1997; Flores-Coto, et al., 2001).

In situ speeds of *C. ignobilis* are within the range of those reported for other perciform species, although most of the available values are for settlement-stage larvae of demersal reef fishes (Trnski, 2002; Leis and Fisher, in press). Further, the rate of increase in speed at 1.6–2.6 cm/s per each mm of growth is similar to that found in the three other perciform species for which there are data (0.3–2.0 cm/s per each mm of growth; Leis et al., 2006). Differences in swimming speed among areas has been reported in a variety of reef fish larvae (Leis and McCormick, 2002); therefore finding a difference for *C. ignobilis* was not unexpected. This variation in behavior among areas and the fact that the rate of increase in speed with growth in the field was less than the increase of U_{crit} in the laboratory clearly demonstrates the complexities of applying laboratory measures to the field, and how behavior in the field can vary with location and situation. The cause for differences in behavior among locations was not clear in our study, but it is only through *in situ* observations that such differences can be discovered.

The approximately linear increase in swimming speed with growth found in *C. ignobilis* was similar to that reported in other species (Fisher et al., 2000; Clark et al., 2005). The ontogeny of endurance in *C. ignobilis* was also linear, in contrast to that of some other species, which are reported to have a strongly concave curvilinear increase in endurance with growth (Fisher et al., 2000; Clark et al., 2005). Perhaps this linearity was the result of studying *C. ignobilis* larger than 8 mm. In other species, preflexion and early postflexion larvae (which we did not study) have very low endurance, but endurance increases rapidly with growth in postflexion larvae.

All our speed measurements were made over periods of 10 minutes or less, but endurance measurements showed that speeds of 10 cm/s can be maintained from several to many hours, enabling distances of up to 40 km to be traversed. The ecological relevance of laboratory measurements of swimming endurance is difficult to assess because, on one hand, these are forced measures of performance, and it is unlikely that larval fishes would swim to exhaustion. On the other hand, endurance measurements are made without rest or food, and are therefore conservative because larvae of other species of the size studied in the present study can swim at least three times farther when fed (Fisher and Bellwood, 2001; Leis and Clark, 2005). In any case, it is clear that *C. ignobilis* larvae can swim for extended

periods at speeds that would make them effective swimmers in many situations. According to the relationship in Figure 4, *C. ignobilis* larvae of about 9 mm could swim without food or rest for about 13 hours (5 km at 10 cm/s) at a speed that is within their observed capabilities *in situ*: this ability increases markedly with growth. Clearly, *C. ignobilis* larvae from a size of 1 cm or less are capable of maintaining speeds of similar magnitude to mean ambient currents for periods of time long enough to strongly influence their dispersal.

Knowledge of vertical distribution of fishes is important because many things vary vertically in the ocean, including current velocity, food concentrations, and predators, all of which can strongly influence survival and dispersal. For these vertically varying factors, the conditions that larval and small juvenile fishes actually encounter are fully under their control because swimming abilities and sensory abilities capable of determining vertical position in the water column develop at a very small size. The *C. ignobilis* we observed in the ocean had considerable control over their vertical distribution, and the depths selected changed with size. Masuda and Tsukamoto (1996) noted ontogenetic changes in preferred light intensity in larvae of *P. dentex*, and it is possible that such changes influence the selection of depth in larval *C. ignobilis*. Two notes of caution are necessary in interpreting the depth-selection behavior and ontogenetic changes in this behavior. The largest larvae were primarily observed at one site, and, it is possible that vertical-distribution behavior varies among areas (Leis, 2004). Secondly, the largest larvae tended to swim to below our safety depth and we therefore do not know if they continued to descend, if they subsequently ascended (in accord with the oscillatory behavior observed in a number of larger individuals), or if they leveled off. In a similar experiment, much larger (60–140 mm) *Pseudocaranx dentex* juveniles initially descended several meters before ascending to a much shallower "preferred depth," usually within 60 seconds (Kuwada et al., 2000). We did not observe such ascents following an initial descent, but we cannot rule out the possibility that they occur for individuals that swam below our safe diving depth (Fig. 5D).

Orientation in the pelagic environment is difficult for fish larvae because of the movement of the water column and the scarcity of reference points in a moving pelagic environment. Orientation is, however, necessary for the arrival of late-stage larvae at nursery habitat and can greatly influence dispersal trajectories (Shanks, 1995; Leis and Carson-Ewart, 2003). Two-thirds of the *C. ignobilis* larvae that we observed swam directionally, as opposed to swimming randomly. This is a somewhat smaller percentage than the 80–100% for directional individuals at the settlement stage for demersal coral reef fishes of similar size (Leis and Carson-Ewart, 2003). Neither the proportion of individual *C. ignobilis* that swam directionally, nor the precision of their directional swimming, increased with growth. The lack of ontogenetic change in individual orientation—in contrast to speed, endurance, and vertical distribution—indicates that orientation ability develops early (at less than 8 mm SL) in *C. ignobilis* larvae. Of course, orientation may improve in individuals larger than those we studied.

The offshore swimming direction of *C. ignobilis* larvae found off the west coast is similar to behavior reported for larvae of some other species at other locations (e.g., Leis et al., 1996; Leis and Carson-Ewart, 2003), but could, in fact, be orientation to the west, rather than offshore. Observations off the east coast would be required to separate the possibilities, and any such test would need to take into account the possibility of temporal factors. The lack of any directionality in Nan Wan Bay is possibly a result of the "U" shape of the bay. Such a bay, where "offshore" constitutes less than half of the possible swimming directions, and where west is onshore, may present challenges to orientation that are greater than those present off an open coast. Alternatively, a bay may offer characteristics that would induce larvae to remain, rather than swim away as they did off the more open coast. Or, older larvae may prefer inshore environments, whereas younger ones do not. The important points, however, are that larvae of 8–15 mm SL demonstrated orientated swimming in the field and that smaller larvae swam in the same direction as larger ones. We can offer only speculation as to the types of cues that *C. ignobilis* may use to orient their swimming, and refer the reader to other sources for this information (e.g., Kingsford et al., 2002; Leis and McCormick, 2002). Our observations on *C. ignobilis* support other research showing that orientation behavior in fish larvae can be location-dependent (Leis et al., 1996; Stobutzki and Bellwood, 1998; Leis and Carson-Ewart, 2003), and if so, this feature add a further complication for attempts to model dispersal.

Our unplanned *in situ* observations of behavior shed light on little-known aspects of the early life history of *C. ignobilis,* which are otherwise difficult to study. Feeding activity by 8–18 mm larvae of *C. ignobilis* was common while they were swimming, as has been found with other species (Leis and Carson-Ewart, 1998). The only larva to encounter a large pelagic fish reacted in the same way as that reported for other species, namely with the apparent goal of moving away from the potential large predator before the small fish could be readily detected (Leis and Carson-Ewart, 2001). Such behavior in a reared individual with no experience with piscivorous fishes indicates that the behavior is not learned. Many carangids associate with jellyfish medusae when small (Shojima, 1962); therefore the brief association we observed between a jellyfish and a 10-mm *C. ignobilis* was not unexpected. *Caranx ignobilis* is considered to be reef-associated during some periods of its life history, but individuals of 9–13 mm do not seem to be inclined to associate with coral reefs. Unlike the larvae of many demersal reef fishes (Leis and Carson-Ewart, 2002), the larval *C. ignobilis* that we observed made no attempt to settle and showed no interest in coral reefs. If anything, *C. ignobilis* moved away from the coral reefs they encountered, although this behavior is not uncom-

mon in larvae of other species (Leis and Carson-Ewart, 1999, 2002). We observed one individual penetrate a thermocline, indicating not only a tolerance for rapid temperature change, but also, that the thermocline is not a barrier to vertical movement for *C. ignobilis*, as has been proposed sometimes for larvae of other species (e.g., Gray and Kingsford, 2003).

We used reared larvae in our study and it is possible that the behavior we observed may have differed from that of wild individuals. Results of studies comparing wild and reared individuals have been inconsistent. Some studies have shown large differences in behavior of reared and wild fishes, the most marked of which involve learned interactions with predators (Brown and Laland, 2001). Differences in swimming performance (in both directions) have been documented in some studies, but not others, or have been present at some developmental stages but not others (e.g., Blaxter, 1975; Dunmall and Shreer, 2003; Smith and Fuiman, 2004). Even if differences in predator-related behavior exist, swimming and orientation are presumably less dependent on experience and learning, and there is less reason to expect them to differ as well. The possibility that reared larvae of *C. ignobilis* may behave differently from wild larvae cannot be entirely dismissed, but the fact that *C. ignobilis* larvae were reared in conditions approaching those found in the field (but with the absence of predators)—kept in large outside ponds at an aquaculture farm and fed a natural assemblage of zooplankton—would presumably make large differences in behavior with their wild counterparts less likely. Unfortunately, we did not have access to wild *C. ignobilis*, and therefore we could not make direct tests; moreover, little is known of behavior in other carangid larvae upon which we might base comparisons.

Caranx ignobilis apparently schools when young (Myers, 1999), and the size range of larvae we studied overlapped with that at which schooling begins in other carangid species (Masuda and Tsukamoto, 1998). We did not attempt to observe schooling in *C. ignobilis*, but it is conceivable that some of the aspects of behavior may differ between individuals that are schooling and those that are solitary.

We observed strong ontogenetic changes in behavior of *C. ignobilis* across a size range of 8 to 18 mm SL. At any size, there was usually a wide range of performances present, and the best performers were able to swim much better than average performers. Given the very high mortality rates experienced by marine fish larvae, the average larva at any given size is unlikely to survive (Cushing, 1990), and it may be only the exceptional performers that do survive. Therefore, it may be more appropriate to use values for the best performers than for average performers in models of dispersal or survival. Increases in swimming abilities with growth were most marked, and significant swimming abilities would probably be present, in larvae as small as 5 mm SL based on extrapolation of performance at size relationships. Ontogenetic changes in vertical distribution behavior were more complex and difficult to interpret, but depth selection seemed to be more variable (both within and among individuals) in larger larvae. We found that orientation behavior of small *C. ignobilis* was already developed and did not increase ontogenetically, although the direction they swam differed between locations. Behavior in small *C. ignobilis* was complex and swimming abilities were well developed. These behaviors are capable of strongly influencing survival and dispersal and show that the larvae of some pelagic fishes have behavioral capabilities similar to those recently documented for larvae of demersal reef fishes (Leis and McCormick, 2002).

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Diurnal and nocturnal temperatures for Atlantic salmon postsmolts (*Salmo salar* L.) during their early marine life

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Abstract—Data storage tags (DSTs) were applied to Atlantic salmon (*Salmo salar* L.) smolts during their seaward migration in the spring of 2002 at a fish counting fence on Campbellton River, Newfoundland. Our objectives were to discover whether or not salmon smolts could carry DSTs and survive, whether or not useful data on thermal habitat could be obtained and interpreted, and whether or not salmon smolts moved vertically in the water column. Data were downloaded from 15 of the recovered tags and revealed the hourly water temperatures experienced by the fish for periods of 3 to 71 days. The data on the DSTs were analyzed for temperature patterns in relation to migration behavior and diurnal movement of the fish. While in the sea, the DSTs recorded night temperatures of 12.5°C, which were higher than day temperatures of 11.6°C; the record from moored recorders, however, indicated that sea temperatures actually declined at night. It is hypothesized that postsmolts avoid avian predators during daylight hours by positioning themselves deeper in the water column and that they were pursuing prey during the deeper vertical descents or ascents noted during the periods of more rapid changes in temperature.

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Our knowledge of the ecology of marine fish, and specifically salmon, at sea has recently been enhanced by information recovered from data storage tags (DSTs) and tracking tags (Sturlaugsson[1]; LaCroix and McCurdy, 1996; Wada and Ueno[2]; Godø and Michalsen, 2000; Reddin et al., 2004). Direct tracking, although valuable, has a number of shortcomings, including the usually short duration of tracking because of the requirement to follow the fish. This short-term tracking often results in interrupted data streams and the added concern that the actual tagging may affect, at least in the short term, the subsequent behavior of the fish (LaCroix and McCurdy, 1996; Walker et al., 2000). Studies of salmon at sea over long periods require new tools and several authors have noted that DSTs are among the least expensive methods of answering some of the questions posed regarding the sea life of salmon. Also, the near extirpation of some stocks, particularly in the Inner Bay of Fundy area of Canada and Maine, U.S.A, requires an explanation of the causative factors (Boehlert, 1997; Anon.[3]; Friedland et al., 2001; Reddin et al., 2004). DSTs should be able to provide better information on the natural behavior of individual fish, their specific habitats, and location over the period of their residence in the sea because of the longer period that information can be collected.

On both sides of the North Atlantic, attention has been recently focused on the downturn in Atlantic salmon stocks and the potential cause or causes (Nickson[4]; Mills[5]; DFO[6];

[1] Sturlaugsson, J. 1995. Migration study on homing of Atlantic salmon (*Salmo salar* L.) in coastal waters W-Iceland—depth movements and sea temperatures recorded at migration routes by data storage tags. ICES C.M. (council meeting) 1995/M: 17, 13 p.

[2] Wada, K. and Y. Ueno. 1999. Homing behavior of chum salmon determined by an archival tag. NPAFC (North Pacific Anadromous Fish Commission Doc. 425, 29 p.

[3] Anon. 1998. Report of the Study Group on ocean salmon tagging experiments with data logging tags. ICES C.M. (council meeting) 1998/G: 17, 34 p.

[4] Nickson, Sir D. 1991. Chairman's report, Atlantic Salmon Trust, progress report, December 1991, 1 p. Atlantic Salmon Trust, Moulin, Pitlochry, Perthshire, Scotland PH16 5JQ.

[5] Mills, D. (ed.). 1996. Enhancement of spring salmon. Proceedings of a one-day conference held in the rooms of the Linnean Society of London; 26 January 1996, 135 p. Atlantic Salmon Trust, Moulin, Pitlochry, Perthshire PH16 5JQ Scotland.

[6] DFO (Dept. of Fisheries and Oceans). 1998. Atlantic salmon abundance overview for 1997. DFO CSAS (Canadian Stock Assessment Secretariat), Stock Status Report D0-02(1998), 22 p.

O'Neil et al.[7]; Anon.[8]). Many authors have noted that information on the sea life of Atlantic salmon (*Salmo salar* L.) may aid in our understanding of the recent increased mortalities that occur at sea compared to those experienced in the 1970s (Mills, 1989; Reddin and Friedland, 1993; Dempson et al.[9]; Jacobsen, 2000; Reddin et al., 2000). In the southern end of the range of Atlantic salmon in North America, declines have been so severe that some stocks are now threatened with extinction and others are currently considered to be extirpated (Marshall et al.[10]). The recent listing of seven salmon stocks in the State of Maine under the U.S. Endangered Species Act and in rivers in the upper Bay of Fundy further underscores the urgency to understand more completely the entire salmon's life history, including the period spent in the ocean. Although the cause (or causes) is unknown, the continued declines in abundance appear directly related to increased mortality at sea, perhaps from predation (DFO, 1998; Cairns and Reddin[11]; O'Neil et al.[7]).

New techniques have recently been applied to the study of salmon in the sea on both sides of the North American continent for Pacific and Atlantic salmon, and recommendations have been made on their future use (Boehlert, 1997; Anon[3]). Although large scale experiments with complex tags are attractive, the high cost per tag and likelihood of low returns, in part due to reduced commercial fishing for Atlantic salmon, have indicated that a smaller scale experiment with inexpensive simple tags may be the best place to start (Anon.[3]). Reddin et al. (2004) demonstrated that these tags when applied to Atlantic salmon adults could provide insight into some aspects of salmon life history.

Overall, the objectives of the present study were 1) to determine if DSTs could be applied to Atlantic salmon smolts and if data could be successfully recovered, 2) to learn more about the thermal habitat of Atlantic salmon during its early marine life, and 3) to test the hypothesis of the commonly held assumption that salmon are mainly surface or near to surface dwellers. This article describes the results of the migration of Atlantic salmon smolts from Campbellton River, Newfoundland, in relation to sea water temperatures recorded by DSTs in 2002.

Materials and methods

Experimental site

Atlantic salmon smolts, defined by Allan and Ritter (1977) as juvenile salmon that are making the transition from freshwater to the marine environment, were obtained in 2002 for tagging from an enumeration fence on Campbellton River, Newfoundland (Fig. 1) where in past years, high numbers were available in early spring (Downton and Reddin[12]). Also, because Campbellton River has a counting fence that is suitable for obtaining counts of adult salmon as they re-enter freshwater, there was a strong possibility of recapturing a returning tagged salmon so that its tag could be recovered (Fig. 1). Smolt and adult salmon have been counted at Campbellton River annually over the last 11 years (O'Connell et al.[13]). In total, there were about 32,600 salmon smolts counted through the counting fence at Campbellton River in 2002, and of these, 311 (~1% of total smolts) were tagged and released with data storage tags (DSTs). Owing to the size and weight of the tags, only smolts over 20 cm fork length were selected for application of tags. Average length of tagged smolts was 25 cm compared to an average length of 18 cm for untagged smolts. Larger smolts were also purposely selected to increase probability of survival.

Tags

The data storage tags (DSTs), sometimes referred to as archival tags, used in this study were iB-4 tags (Maxim/Dallas Semiconductor Corporation, Sunnyvale, CA) and were repackaged for use on fish by Alpha Mach Devices Inc. (Mont St-Hilaire, Québec, Canada). The iB4 tags are small microprocessor-based data loggers embedded in green urethane on which is shown (at bottom right corner of tag) a return address, an identifying number, and the offer of a reward for return of the tag. The iB4 DST records temperature over a range of –5° to 26°C

[7] O'Neil, S., J. Ritter, and K. Robichaud-LeBlanc. 2000. Proceedings of a workshop on research strategies into the causes of declining Atlantic salmon returns to North American rivers. CSAS (Canadian Stock Assessment Secretariat), Proceedings Series 2000/18, 80 p. Department of Fisheries and Oceans, Government of Canada, 200 Kent Street, Stn. 12032, Ottawa, Ontario, Canada K1A 0E6.

[8] Anon. 2003. Report of the Working Group on North Atlantic Salmon. ICES Headquarters, Copenhagen, 31 March–10 April 2003. ICES C.M. (council meeting) 2003/ACFM: 19, 310 p.

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[11] Cairns, D. K., and D. G. Reddin. 2000. The potential impact of seal and seabird predation on North American Atlantic salmon. DFO, CSAS Res. Doc. 2000/012, 36 p.

[12] Downton, P. R., and D. G. Reddin. 2004. Status of Atlantic salmon (*Salmo salar* L.) in Campbellton River, Notre Dame Bay (SFA 4), Newfoundland in 2003. DFO, CSAS Res. Doc. 2004/043, 49 p.

[13] O'Connell, M. F., J. B. Dempson, C. C. Mullins, D. G. Reddin, C. E. Bourgeois, T. R. Porter, N. M. Cochrane, and D. Caines. 2003. Status of Atlantic salmon (*Salmo salar* L.) stocks of insular Newfoundland (SFAs 3-14A), 2002. CSAS Res. Doc. 2003/002, 63 p.

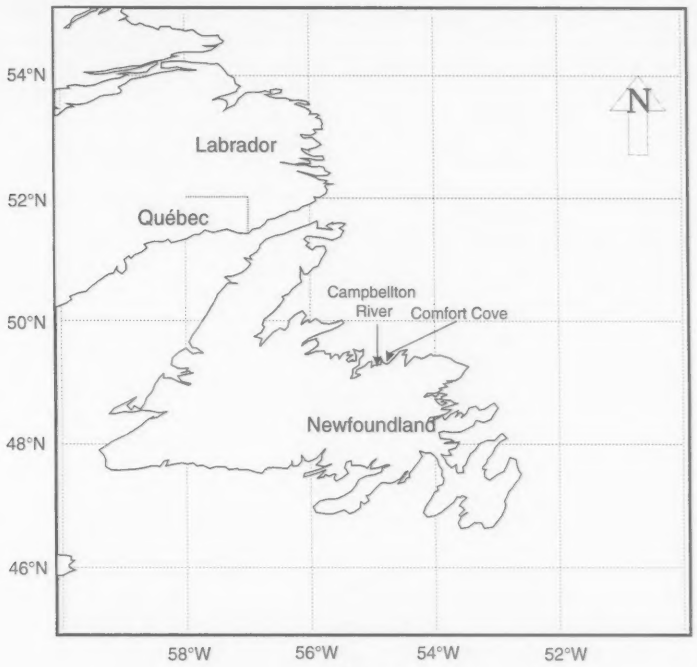

Figure 1

Map of Newfoundland, Labrador, and Québec showing the release location at Campbellton River for Atlantic salmon (*Salmo salar*) smolts with data storage tags attached.

with a precision of ±1°C and an accuracy of 0.15°C. The iB4 data storage tag will store up to 2048 readings but the number of data recorded by each tag depends on the length of time that the tag was at large and the sampling rate of the tag. Our iB4 tags were set to start on the day of tagging and record a temperature every hour—a sampling rate that would allow for 85 days of temperature recordings. Tags were calibrated by the manufacturer and checked for accuracy on return. A tag weighs 5.5 g in air and less than 2.6 g in water, is approximately 24 mm by 17 mm by 8 mm, and has a hole at either end for attachment to a fish. Tag programming, data acquisition, and data downloading were achieved by the user with a connecting clamp interfaced to the serial adapter on any standard IBM compatible computer. No correction for drift in the time function was made because of the short period over which the experiment took place (Walker et al., 2000; Reddin et al., 2004). Tags were attached to salmon smolts by using a double-wire (0.32 mm stainless steel) bridal that was passed through the dorsal musculature and that was anchored to the fish by means of a backing plate on the opposite side of the fish. A reward of $10 Canadian was offered for the return of the tag. The smolts were anaesthetized with clove oil, tagged, and placed in holding tanks in the river and given an approximate 10-hour recovery period before release in the evening on the downstream side of the counting fence. All smolts survived the tagging process. From 311 salmon tagged and released, 15 DSTs were recovered with data intact. All tagged fish were recovered during the year of tagging.

Data analysis

Temperature data recorded by the recovered DSTs were analyzed and compared to oceanographic and freshwater temperature data collected during the summer of 2002. The freshwater data was recorded by a Hugrun temperature recorder (Hugrun, Sidumuli 13, Reykjavik 108, Iceland) placed in the trap at the Campbellton River counting fence, and the sea temperatures came from Hugrun recorders placed just outside the estuary of Campbellton River at 8 m depth and from another at Comfort Cove at 10 m, both reported by Colbourne[14] (Fig. 1). Periods of daylight and darkness were estimated from the U.S. Navy Observatory[15] online photoperiod calculator. Latitudinal and longitudinal positions

[14] Colbourne, E. 2003. Physical oceanographic conditions on the Newfoundland and Labrador Shelves during 2002. DFO, CSAS Res. Doc. 2003/020, 57 p.

[15] U. S. Naval Observatory, Astronomical Observations Department. 2004. Website: http://aa.usno.navy.mil/data/docs/RS_OneDay.html [accessed on 7 March 2006.]

used to calculate sunrise and sunset for individual fish were based on the latitude and longitude at the mouth of Campbellton River. Although it varies by date, day at the latitude of Campbellton River during summer generally occurs from 0500 hours to 2300 hours and night occurs from 2300 to 0500 hours local time. Each individual temperature record from the tags in Greenwich Mean Time (GMT) was then coded to either day or night. Some salmon smolts in Newfoundland return to their home rivers within a couple of months of migrating to sea as precocious postsmolts and as postsmolts cannot travel extensively from the area of the river mouth, so that the river mouth provides a proxy position to determine day length (Downton and Reddin, 2004). Standard weeks were assigned with the Microsoft Excel function WEEKNUM. The analysis of variance technique used to test for temperature differences between fish was the PROC MIXED procedure in SAS (SAS Institute Inc., Cary, NC) The model treated tag as a random rather than a fixed variable. Day temperatures were compared to those at night and any diurnal vertical movements were considered to be reflected by sudden changes in temperatures. Newfoundland coastal waters always exhibit vertical stratification in late spring and early summer.

Results

Tag and data recovery

In total, temperature records were recovered from 15 of the 18 tagged Atlantic salmon smolts for an overall return rate of 5.8% (Table 1). Of the 18 recovered tags, 13 came from herring nets during the same summer that the fish were released. Average days free for those DSTs recovered in herring bait nets was 14 days and all were recovered within Indian Arm into which Campbellton River flows. In addition, two were recovered at the counting fence, one was recovered during a swimming survey of the lower portion of the river, one was angled, and another was found by a swimmer a full year after the fish was tagged and released. The great number of tags recovered in herring gear was due to tags becoming entangled in the nets. The longest period of recorded water temperatures while fish were free swimming was 71 days and the shortest was 3 days (Table 1). All tags were recovered during the first summer after their release, except the one found by the swimmer.

Water temperature profiles

Temperatures were recorded every 60 minutes for all recovered tags. The overall sampling frequency or the number of data points collected per tag ranged from a low of 32 for DST257 to a high of 1681 for DST45 and the second longest was for DST267 with 1373 (Table 1). The most complete records were recorded by DSTs 45 and 267 because the fish to which they were attached spent the least amount of time in freshwater and returned to freshwater after spending a minimum of eight weeks at sea. Both of these fish returned at 0+ sea age, a trait which is observed in about 15% of the salmon returning to Campbellton River in recent years (Downton et al., 2004). The water temperature profiles from the DSTs revealed a complex pattern of daily variations (Figs. 2–4). A number of points of interest can be made from the individual DST records. The temperature records from the DSTs when compared to local freshwater and marine temperatures allowed the time of day to be ascribed for most fish when the transition from the river to sea occurred (Fig. 3). The records indicated that 8 out of 13 fish made the transition from freshwater to the sea during daylight, whereas both fish recovered at the counting fence after spending time at sea re-entered freshwater during the night. Because they had the longest period of free swimming activity recorded on the DSTs, tags 45 and 267 were selected for further analysis including comparison for freshwater and sea temperatures (Fig. 3). Within the daily variations, temperature profiles from individual DSTs showed several prominent features:

1 a period of freshwater residence during which time the freshwater and DST temperatures corresponded closely, followed by entry into the sea at which time the temperatures recorded by the DSTs diverged from the recorded freshwater temperatures (Fig. 4, A and B);
2 a period of low variability in temperature fluctuations at the beginning of the marine record (with a coefficient of variation of less than or equal to 10%), continuing for at least a couple of weeks (Fig. 4C);
3 after the period of low variability, a series of rapid daily changes in temperature from either warm to cool or, for a few limited cases, from cool to warm (with coefficients of variation of greater than 30%) (Fig. 4, D and E) and during this period, DST temperatures sometimes varied by as much as 13°C over a couple of hours;
4 a distinct trend to increasing temperatures as the summer progressed which was due to gradual heating of the surface layer and deepening of the thermocline (Fig. 3); and
5 a series of steady temperatures near the end of the ocean period before entry into freshwater (with coefficients of variation of less then 12%) (Fig. 4F).

Between the periods of low temperature variability at the beginning and end of the various series, there was a period of rapid changes in temperature when the fish were assumed to have dived deeper in the water column, followed by ascents to near surface. The frequency of these rapid changes in temperature provides some information on the number of dives per day which numbered between 1 and 3 and may be a proxy for the length of time spent feeding and chasing after prey or fleeing from predators.

Table 1

Release and recovery details for eighteen iB-4 data storage tags (DSTs) applied to Atlantic salmon (Salmo salar) smolts at Campbellton River, Newfoundland, 2002. N/A= data were not available.

DST number	Number of records	Date and time tag was turned on	Date and time when tag was recovered	Fork length (cm)	Return date	Days free	Comments
22	327	5/17/02 8:20	5/17/02 8:20	22.0	spring, 2002	15	Caught in herring bait net in Indian Arm Tag found 25 m below counting fence site
43	N/A	5/19/02 7:59	5/19/02 9:28	24.0	24 May 2002	—	No fish was attached to tag
45	1681	5/19/02 8:06	5/19/02 9:36	28.0	28 Jul 2002	71	Caught at the upstream counting fence
55	N/A	5/19/02 8:30	5/19/02 10:19	27.0	03 Jul 2003	—	Found in estuary by swimmer
74	N/A	5/21/02 8:46	5/21/02 10:23	23.0	spring, 2002	—	Caught in herring bait net in Indian Arm
84	180	5/23/02 10:40	5/23/02 15:32	26.0	spring, 2002	8	Caught in herring bait net in Indian Arm
97	305	5/24/02 8:16	5/24/02 10:30	24.0	spring, 2002	14	Caught in herring bait net in Indian Arm
98	588	5/24/02 8:21	5/24/02 10:30	27.5	spring, 2002	26	Caught in herring bait net in Indian Arm
103	302	5/24/02 8:36	5/24/02 10:30	26.0	spring, 2002	14	Caught in herring bait net in Indian Arm
107	634	5/24/02 9:09	5/24/02 10:30	26.0	spring, 2002	28	Caught in herring bait net in Indian Arm
129	562	5/26/02 8:21	5/26/02 11:00	25.0	spring, 2002	25	Caught in herring bait net in Indian Arm
195	213	5/30/02 9:08	5/30/02 10:48	26.0	spring, 2002	10	Caught in herring bait net in Indian Arm
238	133	6/1/02 8:12	6/1/02 10:14	25.0	spring, 2002	7	Caught in herring bait net in Indian Arm
245	129	6/2/02 7:35	6/2/02 9:04	25.0	spring, 2002	6	Caught in herring bait net in Indian Arm
247	401	6/2/02 7:39	6/2/02 9:12	24.0	19 Jun 2002	17	Angled upstream
257	32	6/2/02 8:07	6/2/02 9:56	25.0	spring, 2002	3	Caught in herring bait net in Indian Arm
267	1373	6/2/02 8:29	6/2/02 10:49	34.0	30 Jul 2002	59	Recovered by upstream counting fence
293	240	6/4/02 6:59	6/4/02 9:50	26.0	spring, 2002	11	Caught in herring bait net in Indian Arm

Thermal ecology

A comparison of temperatures for night and day for the two tag recoveries with detailed data indicated differences between daily night and day temperatures for weeks 24 to 29 (11 June–22 July) (Fig. 5). The tagged salmon appeared to be at lower temperatures during the day than at night. Although there were only slight differences between day and night for the cumulative temperatures in some weeks (i.e., week 24 [11–17 June]), for others the differences were quite large (i.e., week 27). These differences were reflected in the overall mean of 12.5°C at night compared to the overall mean of 11.6°C during the day—values which are significantly different from each other ($t = -6.32$, $P<0.0001$) and which possibly reflect temperatures at different depths. Although there was some variation among fish, this pattern was gener-

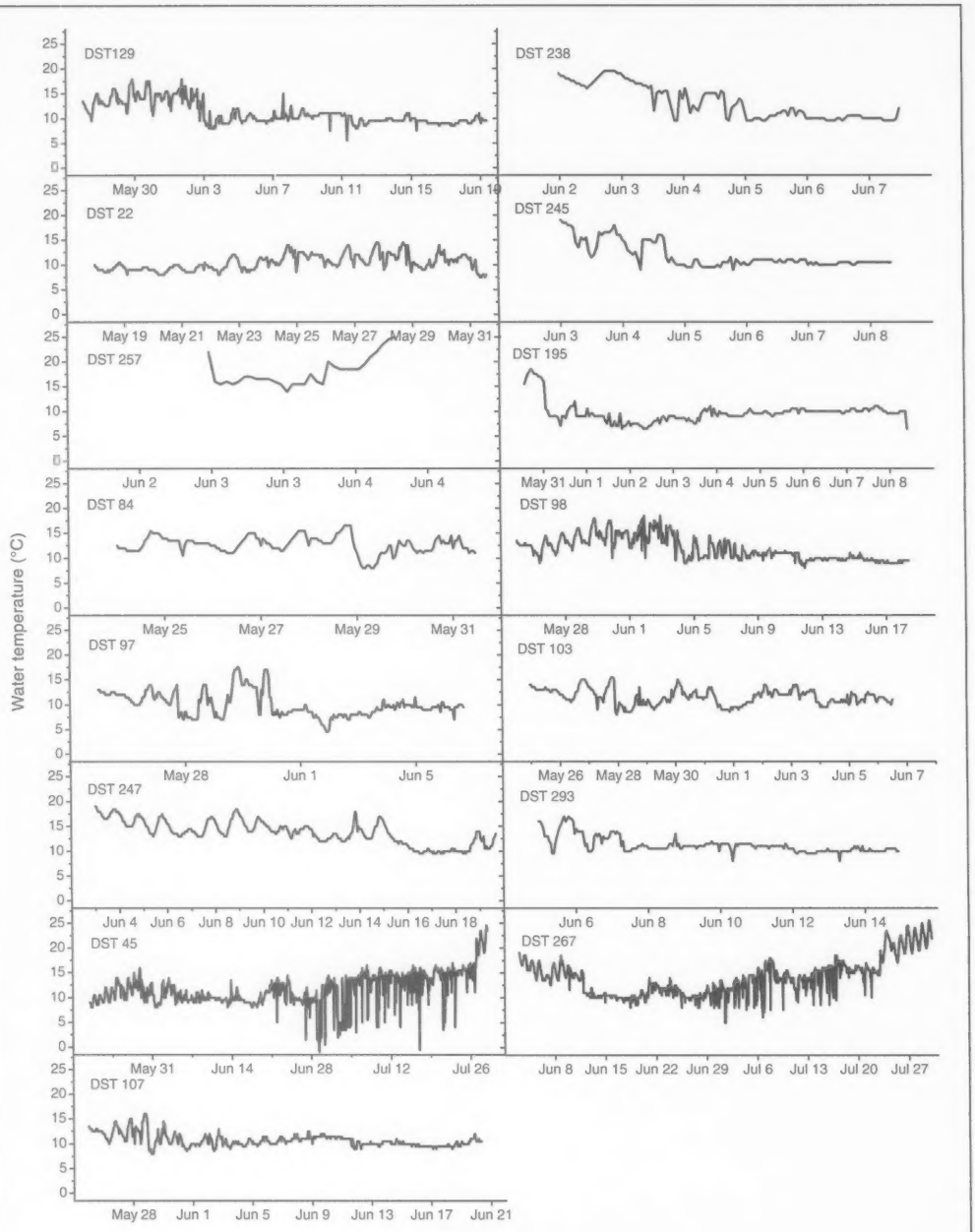

Figure 2

Hourly temperatures and dates recorded by 15 data storage tags attached to Atlantic salmon (*Salmo salar*) postsmolts at Campbellton River, 2002.

ally consistent. The cooler temperatures experienced by the fish during the day indicated that they were deeper in the water column during day than during the night. Diurnal trends in water temperatures also have to be considered because stream temperatures are generally warmer during the day than at night. Warmer temperatures during the day are generally the case for sea temperatures as well (t=5.00, P<0.0001) although less

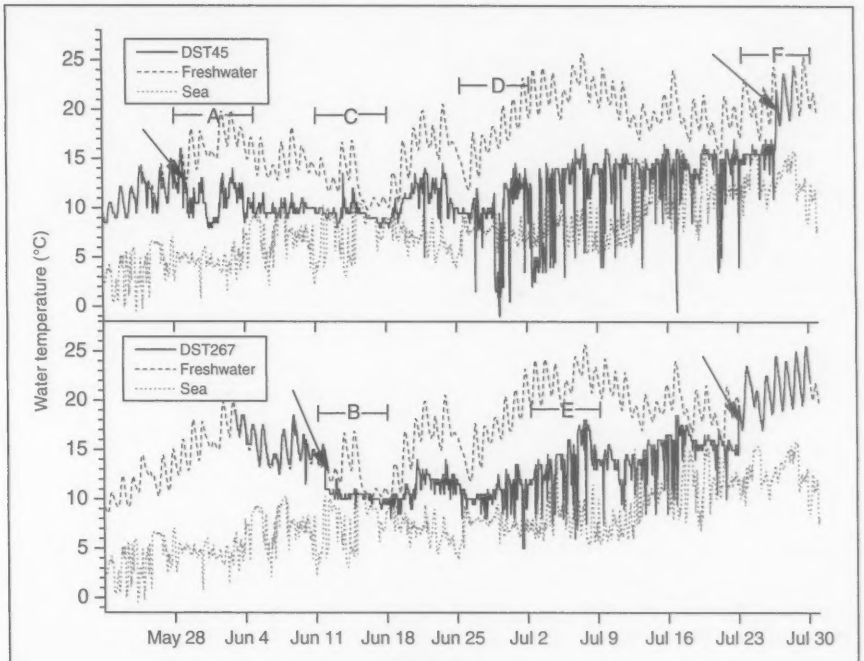

Figure 3

Hourly temperatures recorded by data storage tags on Atlantic salmon (*Salmo salar*) postsmolts versus date for tags 45 and 267 applied at Campbellton River, 2002. Also shown are water temperatures recorded at the trap in the Campbellton River counting fence and in the sea near the Campbellton River estuary, 2002. Arrows indicate time of departure from and entry to freshwater. Periods selected for further analysis are shown and labelled alphabetically from A to F and are shown in detail in Figure 4.

pronounced at greater depths. Because sea temperatures are lower at night than during the day and because the water temperatures experienced by the fish are warmer at night, it is likely that the fish are actively changing depths. Also, there were times when water temperatures declined or increased by 5°C but the temperature of the fish remained steady; this feature would indicate that the fish was actively seeking specific temperatures and changing position in the water column in order to find these temperatures.

The results of the mixed-effects ANOVA with data for weeks 24 to 29 from fish tags 45 and 267 indicated significant differences in temperature for week ($F_{5, 1987}$=251.82, P<0.0001) and night-versus-day effects ($F_{1,2393}$=54.53, P<0.0001). Both smolts spent about 90% of the time in water temperatures ranging from 8° to about 15°C. Overall, mean temperature for day activities for both fish combined was 11.6°C and for night it was 12.5°C. Therefore, for all weeks for both fish, temperatures experienced during the day were generally lower than during the night. Whether these differences were due to choice or simply because the fish were in different locations and experiencing local water conditions is unknown.

The frequency distribution of water temperatures while the fish were in the sea showed a wide range, from below 0° to about 20°C (Fig. 6). This distribution was wider and included temperatures that were both colder and warmer than temperatures available in the estuary off Campbellton River at 8 m or at Comfort Cove at 10 m. The warmer temperatures in the estuary than those recorded by the sea recorders are possibly due to the fish being near the surface or shore (or to both factors). The DST temperatures were lower than freshwater temperatures, reflecting the sea temperatures rather than freshwater temperatures. The pattern for each fish presumably reflects a combination of individual preferences and the availability of specific water temperatures depending on the location of the fish at sea. The temperatures recorded by each tag reflect the time (season) of entry into the sea and the time of recapture, especially for those fish caught in fisheries while the fish were still at sea.

Discussion

The transition from freshwater to ocean life for Atlantic salmon (whether as smolts or kelts) can have a serious

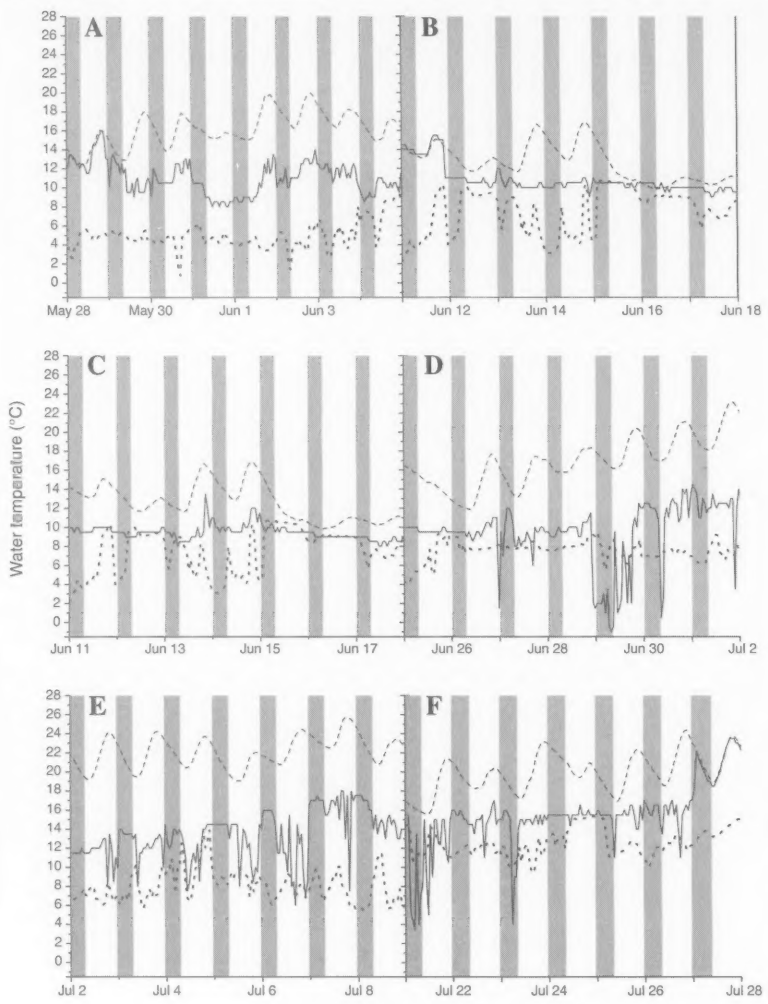

Figure 4

Comparison of day and night temperatures recorded hourly by data storage tags on Atlantic salmon (*Salmo salar*) postsmolts for selected periods of time. Night is shown in grey and day is shown in white. Solid lines are the DST temperatures; the dashed line represents freshwater temperature and dotted line represents sea temperature at 8 m. The periods A to F are shown on Figure 3 for each tag.

consequence for an individual fish, as well as be an important factor controlling year-class strength and abundance at the population level (McCormick and Saunders, 1987, McCormick et al., 1998). The transformation process from freshwater to salt water made by smolts is accompanied by changes in metabolic rate (Hoar, 1988) and increases in energy demands, which explain the need for the fish to immediately begin feeding. Levings (1994) concluded that of all the variables influencing survival of postsmolt salmon, temperature is particularly important. If they are to survive, individuals must quickly adapt to their new physical environment and be able to flee predators and seek prey. In spite of its presumed importance, the ecology of salmon smolts as they enter the marine environment is largely unknown. This article provides the first recorded results of temperatures experienced by salmon smolts as they enter the sea and provides insight into how postsmolts adapt to life at sea based on ambient temperature ranges and temperature choices made by the postsmolts. The

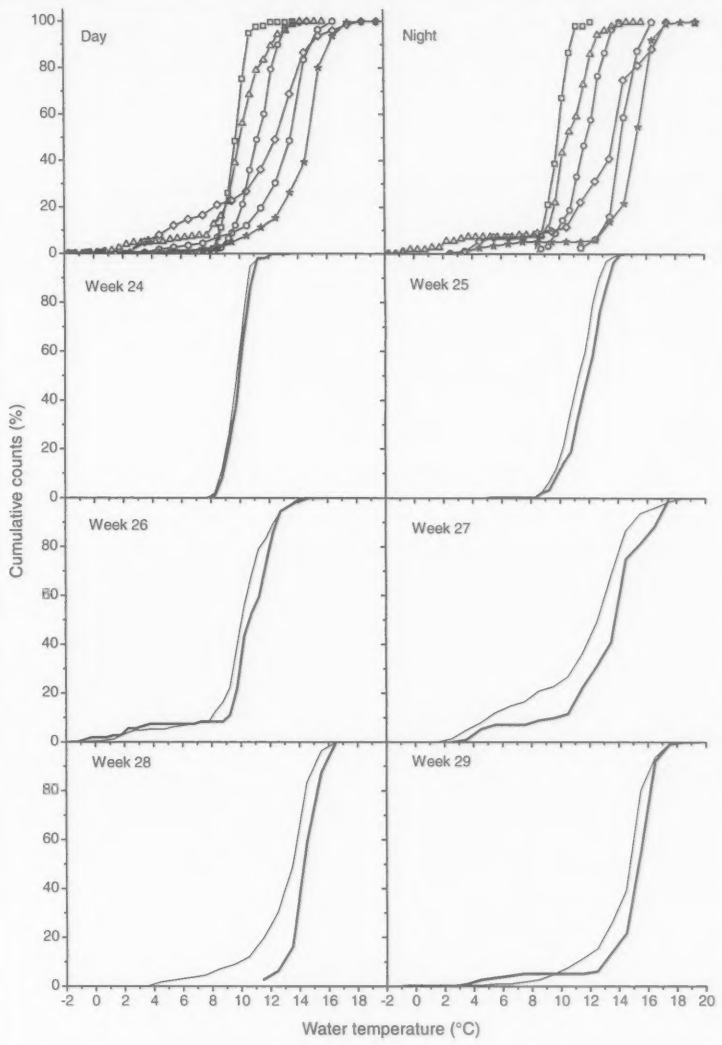

Figure 5

Difference between night and day temperatures recorded hourly by data storage tags and expressed as cumulative counts for weeks 24 to 29 from Campbellton River, 2002. Water temperatures are shown for six periods and for all day and night temperatures. Thin solid line is for daytime temperatures and thick line is for night time temperatures. In the multi-line graphs labelled "day" and "night," the square=week 24, the circle=week 25, triangle=week 26, polygon=week 27, dark pentagon=week 28 and the star=week 29.

temperature profiles collected by these data storage tags provide detailed information on the thermal habitat experienced by 15 Atlantic salmon postsmolts for periods ranging from a few days to about two months at sea. Temperatures recorded ranged from below 0° to nearly 20°C, although most of the time was spent in water from 8° to 15°C, probably near the surface.

Sigholt and Finstad (1990) and Handeland et al. (2003) reported that lethal sea water temperatures for both wild and farmed salmon smolts adapting to seawater occurred at very low and very high temperatures. At the lower end of the range in temperatures, some mortalities occurred at sea temperatures of 6–7°C, whereas at the higher end, mortalities occurred at temperatures

over 14°C, indicating that there may be environmental windows for successful transition of smolts into the sea at locations other than at the extreme edges of the temperature ranges documented by Power et al. (1987). Reddin and Friedland (1993) noted that during colder years with heavy ice flows along the northeast coast of Newfoundland, commercial catches and returns of salmon to rivers were lower, even though freshwater warming was occurring normally and they also noted that these low catch rates and returns may have been due to the mortality of postsmolts early in the marine phase. Our results from DSTs applied to Campbellton River smolts indicated that temperature-related mortalities, at least in 2002, were unlikely because the smolts spent little time in water colder than 7°C. Furthermore, because the only colder water present was deeper in the water column, salmon postsmolts were able to avoid it by remaining in the warmer surface waters. In 2002, there was little or no inshore ice at the time of the Campbellton River smolt migration as is sometimes present in other years when mortalities from cold water temperatures could occur.

It is interesting to note that temperatures recorded by the DSTs for the first few weeks after the smolts entered the sea were very similar to that experienced by salmon kelts tagged with DSTs also from Campbellton River (Reddin et al., 2004). In addition, the temperatures from tagged kelts when compared to temperatures from tagged smolts showed similar periods of stability just after entry of the salmon into the sea, as well as abrupt changes in temperatures consistent with deep diving activities. Although we did not know the precise geographic location of either group of fish, it appears that kelts and postsmolts are found initially in water of similar temperatures and behave in similar ways with respect to temperature. Because neither the postsmolts nor kelts started their deep diving activities for four weeks after sea entry, it may be that they were recovering from the transition process or that they may have been near shore where deeper depths are not available (or both these reasons may apply). Resolution of these questions will have to await the results from application of geolocation and depth-sensing tags.

Colbourne et al.[16], Friedland et al. (2003), Beamish and Bouillon (1993), and Downton and Miller (1998) and many others have examined relationships between environmental variables and the abundance of Pacific and Atlantic salmon and other fish species with a view of providing forecasts of future abundance but without any knowledge of what thermal regimes the fish actually use. Colbourne et al.[14] indicated that the goal of searching for relationships is important in order that

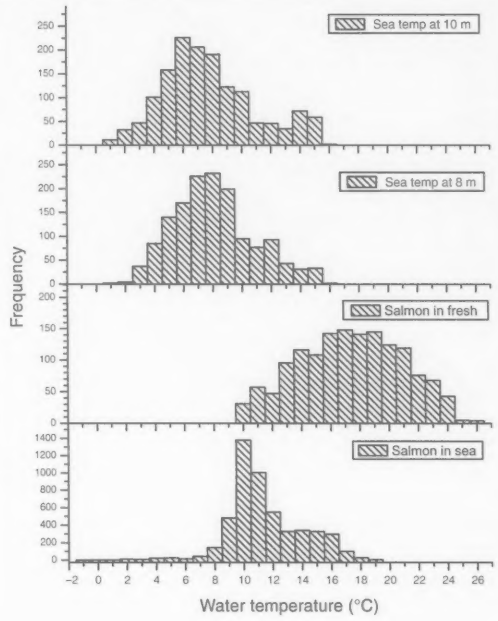

Figure 6

Frequency distributions for all temperatures recorded hourly at sea at 10 m depth (Sea temp at 10 m) and at 8 m depth (Sea temp at 8 m), and for salmon in freshwater from the DSTs (Salmon in fresh), and for salmon from DSTs while in the sea (Salmon in sea). All sea temperatures from the DSTs were used and the freshwater and marine temperatures are for the same time periods that the DST-tagged fish were in the sea.

influences of the physical ocean environment can be used to provide more accurate forecasts of stock abundance and ultimately so that they can be used to create management plans for various fisheries (Bisbal and McConnaha, 1998; Friedland, 1998). These predictions are currently used for both North American and European Atlantic salmon, for which abundance has been forecasted partly on the basis of environmental information (Anon.[8]). Physical conditions in the ocean have been shown to be related to mortality and growth of some other species (Brander, 1995; Dutil et al., 1999; Watanabe and Yatsu, 2004). Blackbourn (1993) and Downton and Miller (1998) have suggested that freshwater survival rates for some species of Pacific salmon are even related to SSTs experienced by potential spawners while still at sea, shortly before their return to freshwater. These studies and their importance clearly show the need for studies on the physical oceanography and ecology of fish at sea. For Atlantic salmon, Reddin and Friedland (1993) created a profile of sea temperatures, based on research vessel catch rates, that indicated that Atlantic salmon were commonly found in water at temperatures from 4° to 10°C. Reddin et al. (2004)

[16] Colbourne, E. B., E. G. Dawe, D. G. Parsons, E. F. Murphy, W. R. Bowering, E. L. Dalley, J. T. Anderson, J. B. Dempson, D. Orr, D. E. Stansbury, and G. P. Ennis. 2002. A preliminary review of environmental-stock relationships for some species of marine organisms in NAFO waters of the Northwest Atlantic. NAFO SCR Doc. 02/34, 21 p. Northwest Atlantic Fisheries Organization, P.O. Box 638, Dartmouth, Nova Scotia, Canada B2Y 3Y9.

indicated that Atlantic salmon kelts tagged with DSTs were found where temperatures ranged from a low near 0° to over 25°C, although most of their time was spent in water of 5° to 15°C. This finding was similar to that for adults by Sturlaugsson[1] and Karlsson et al.[17] The present study indicates that salmon postsmolts are located mostly near the surface in water temperatures ranging from 8° to about 15°C. Because the temperatures experienced by kelt are somewhat warmer then those used in correlation studies of salmon growth and survival, it may be that our results will encourage other researchers to review the temperatures they use in such studies.

Prey items in the diet of adult Atlantic salmon are fairly well known revealing that Atlantic salmon are opportunistic feeders, feeding on whatever is abundant in the area (Reddin, 1988; Hislop and Shelton, 1993). Although food resources are still unknown for some regions, the prey species of smolts and postsmolts at sea has recently become an important area for research in the northeast Atlantic (Andreassen et al., 2001; Salminen et al., 2001; Rikardsen et al., 2004). Rikardsen et al.'s (2004) extensive analysis of postsmolt diet in eight fjords in Norway revealed extensive feeding on pelagic larval fish species and crustaceans, as well as substantial geographic and annual variation in prey diversity and feeding intensity. Furthermore, Levings (1994) summarized the diet of smolts and postsmolts in the estuarine and near-shore environments from publications by Power and Shooner (1966), Dutil and Coutu (1988), and Hvidsten et al.[18] which shows postsmolts feeding on gammarid amphipods and intertidal and land-based insects. Although diet information exists for postsmolts, the feeding mechanisms of postsmolts are unknown because there are few, if any, tracking studies in estuaries and the coastal areas. However, the new data on postsmolts early in their marine life that we have collected using DSTs can help us infer this information and the diet studies, although not specific to Newfoundland waters, indicate that salmon prey on pelagic fish larvae and crustacean species, some of which inhabit the deeper waters of the water column. Thus, it would appear that postsmolts in the present study and the kelts in a previous study (Reddin et al., 2004) were diving from surface waters to greater depths to obtain prey. The temperature profiles from the DSTs, compared to oceanographic data available from other studies (Colbourne[14]; Colbourne and Fitzpatrick[19]), indicate that these dives may be anywhere from 25 to 50 m in depth.

There is a tendency for postsmolts to be caught in the upper part of the water column, as evidenced by trawling for postsmolts at sea (Shelton et al., 1997; Holm et al., 2000; Rikardsen et al., 2004), by acoustic tracking of postmolts in fjords (Holm et al., 2000; Moore et al.[20]), and by net catches in surface waters (Dutil and Coutu, 1988; Reddin and Short, 1991; Thorisson and Sturlaugsson[21]). The temperature profiles from our DST-tagged postsmolts indicate that although most of their time is spent near the surface (and nearer the surface at night), salmon postsmolts undergo deeper dives, probably in search of prey. Deeper diving activities have been reported previously for salmon kelts also from Campbellton River by Reddin et al. (2004). The present study demonstrates that postsmolts also show the same type of behavior although the frequency of dives varies somewhat from fish to fish. Holm[22] et al. (2000) noted that salmon postsmolts caught in pelagic trawls in the Norwegian Sea were all caught during surface trawls; none were caught at deeper depths. Westerberg (1982) during coastal tracking studies noted that salmon made dives of short duration to greater depths; his results are similar to the results shown in our study.

Wada and Ueno (1999) listed three hypotheses to explain diving behaviour in Pacific salmon, viz. the salmon are making orientation for homing migration, for feeding, and for controlling body temperature. Reddin et al. (2004) suggested a fourth hypothesis: that the salmon are diving to avoid predators. Our conclusion is that the deep diving activities of salmon postsmolts (to as deep as 50 m) recorded by the DSTs, because of their frequent nature, are probably related to prey seeking and feeding. Reddin et al. (2004) further pointed out that there may be an energetic advantage for salmon to seek prey in cooler, deeper waters where prey are more abundant and then to return to warmer surface waters where their food can be digested more rapidly.

Ecological information can also be discerned from the temperature patterns provided by the DSTs. Ogura and Ishida (1995), Wada and Ueno (1999), Walker et al. (2000) and Reddin et al. (2004) all noted a period of more stable temperatures experienced at both the beginning and at the end of the temperature time series from the DSTs and concluded that the fish remained at the same

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[19] Colbourne, E. B., and C. Fitzpatrick. 2003. Physical oceanographic conditions in NAFO subareas 2 and 3 on the Newfoundland and Labrador Shelf during 2002. NAFO (North Atlantic Fisheries Organization) SCR Doc. 03/14, 57 p. Northwest Atlantic Fisheries Organization, P.O. Box 638, Dartmouth, Nova Scotia, Canada B2Y 3Y9.

[20] Moore, A., I. C. Russell, M. Ives, E. C. E. Potter, and C. P. Waring. 1998. The riverine, estuarine and coastal migratory behaviour of wild Atlantic salmon (*Salmo salar* L.) smolts. ICES CM 1998/N: 16, 11 p.

[21] Thorisson, K. and J. Sturlaugsson. 1995. Postsmolt of ranched Atlantic salmon (*Salmo salar* L.) in Iceland: IV. Competitors and predators. ICES C.M. 1995/M: 12, 9 p.

[22] Holm, M., I. Huse, E. Waatevik, K. B. Døving, J. Aure. 1982. Behaviour of Atlantic salmon smolts during the seaward migration. I. Preliminary report on ultrasonic tracking in a Norwegian fjord system. ICES CM 1982/M:7, 10 p.

location in the water column for some period of time, perhaps adjusting to the presence of the tag or to life in the sea (or to both). Furthermore, Reddin et al. (2004) noted that this period of temperature stability could be also due in some instances to the fish being near shore in shallow water where large scale vertical movements and their concomitant changes in temperature were not possible. This period of restricted vertical activity seemed to cease as the fish made its return migration towards freshwater. Our study indicates that in freshwater the water temperature recorded at the trap corresponds closely to the temperature recorded by the DST on the fish on its departure from the river and at its return. DST temperatures in freshwater follow the diurnal rhythm of warming and cooling of the river. In the sea, there is a period of stable temperatures with a diurnal rhythm that follows the daily warming and cooling. Next, the smolts began a period of fairly rapid descents and ascents in the water column during which temperatures rose and fell much more quickly then during the natural daily cycle. Also, night temperatures were warmer than day temperatures, in contrast to the daily warming and cooling cycle of the sea, indicating that smolts were higher in the water column at night then during daylight hours. The differences in temperatures between day and night may reflect avoidance of avian predators as suggested by Reddin et al. (2004) and Montevecchi et al. (2002). This finding is similar to that shown for adult chum salmon by Friedland et al. (2001) but contrasts with that reported by Shelton et al. (1997) who reported that no catches of postsmolts occurred at night during surface trawling in the northeast Atlantic. Because the records of trawling at night are sparse, we recommend that more effort should be put into night trawling in light of the information from our DST-tagged postsmolts.

In terms of our objectives, we have shown that Atlantic salmon smolts can carry DSTs, and that a sufficient number of tags with useful data on thermal ecology can be successfully recovered. The return rates were low and validated the preliminary use of the less expensive DSTs but were high enough that these experiments could be repeated elsewhere. The use of more expensive DSTs with geoposition and more environmental sensors will require methods to recover them at sea if sufficient tags are to be available to provide meaningful results. The thermal habitat used by Atlantic salmon is shown; postsmolts are found in water with temperatures ranging from 8° to about 15°C in the spring. Lastly, although we show from the water temperature records that salmon postsmolts are frequently found near the surface, it is also evident that they make frequent deep dives of short duration. We hypothesize that these deep dives may be directly related to feeding or to evasion from predators (or to both), as has been observed for kelts by Reddin et al. (2004).

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A prior for steepness in stock-recruitment relationships, based on an evolutionary persistence principle

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Abstract—Priors are existing information or beliefs that are needed in Bayesian analysis. Informative priors are important in obtaining the Bayesian posterior distributions for estimated parameters in stock assessment. In the case of the steepness parameter (h), the need for an informative prior is particularly important because it determines the stock-recruitment relationships in the model. However, specifications of the priors for the h parameter are often subjective. We used a simple population model to derive h priors based on life history considerations. The model was based on the evolutionary principle that persistence of any species, given its life history (i.e., natural mortality rate) and its exposure to recruitment variability, requires a minimum recruitment compensation that enables the species to rebound consistently from low critical abundances (N_c). Using the model, we derived the prior probability distributions of the h parameter for fish species that have a range of natural mortality, recruitment variabilities, and N_c values.

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Success in parameter estimation for stock assessment models often requires sufficient data and correct specification of prior distributions for the estimated parameters (Punt and Hilborn, 1997; Needle, 2002). This is especially true for successfully estimating stock-recruitment relationships with stock assessment models because there often are not sufficient data and there is considerable variability in stock-recruitment relationships. Even in the cases where there are sufficient data, these data can be very noisy and may not show a clear pattern for fitting stock-recruitment relationships (Hilborn and Walters, 1992; Williams and Shertzer, 2003; Munch et al., 2005). Yet, stock-recruitment relationships are important in making fisheries management decisions, especially for over-fished stocks such as widow rockfish (*Sebastes entomelas*), bocaccio (*Sebastes paucispinis*), and darkblotched rockfish (*Sebastes crameri*) along the west coast of the United States (He et al.[1]; MacCall[2]; Punt, 2003; Rogers[3]). Stocks with low values of steepness have low recruitment compensation; therefore stocks will take a long time to rebuild from over-fished status to desired management levels even though total allowable catches for these stocks are kept small (Mace and Doonan[4]).

In this study, we used a simple population model to derive prior distributions (referred to hereafter as "priors") for the steepness parameter (hereafter denoted h) (Mace and Doonan[4]). Prior distributions are probability distributions that represent existing information about parameters. The model was based on the principle that persistence of any fish species, given its life history and its exposure to recruitment variability,

[1] He, X., S. V. Ralston, A. D. MacCall, D. E. Pearson, and E. J. Dick. 2003. Status of the widow rockfish resource in 2003. Vol. 1: Status of the Pacific coast groundfish fishery stock assessment and fishery evaluation, 138 p. Pacific Fishery Management Council, 7700 NE Ambassador Place, Portland, OR.

[2] MacCall, A. D. 2003. Status of bocaccio off California in 2003. Vol. 1: Status of the Pacific coast groundfish fishery stock assessment and fishery evaluation, 56 p. Pacific Fishery Management Council, 7700 NE Ambassador Place, Portland, OR.

[3] Rogers, J. B. 2003. Darkblotched rockfish (*Sebastes crameri*) 2003 stock status and rebuilding analysis. Vol. 1: Status of the Pacific coast groundfish fishery stock assessment and fishery evaluation, 56 p. Pacific Fishery Management Council, 7700 NE Ambassador Place, Portland, OR.

[4] Mace, P. M., and I. J. Doonan. 1988. A generalized bioeconomic simulation model for fish dynamics, 47 p. New Zealand Fishery Assessment Research Document 88/4. Fisheries Research Center, P.O. Box 297, Wellington, New Zealand.

would require a minimum recruitment compensation to allow the species to rebound from low abundances. We argue that distribution of the h parameter for any species could be determined from its life history and recruitment variability. Using the model, we derived the prior distributions of h for fish species that have a range of natural mortality, recruitment variabilities, and low critical abundance (N_c) values.

Methods

In calculating steepness priors, we used a simple population model with a Beverton-Holt stock recruitment relationship:

$$N_{(t)} = N_{(t-1)}e^{-M} + \frac{N_{(t-1)}}{\alpha+\beta N_{(t-1)}} e^{\left(R_{(t)}-\frac{\sigma^2}{2}\right)}, \quad (1)$$

where $N_{(t)}$ = population size at year t;
M = natural mortality;
α and β = recruitment parameters; and
$R_{(t)}$ = the logarithm recruitment residual at year t that follows a normal distribution of $N(0, \sigma^2)$, where σ is recruitment variability (Hilborn and Walters, 1992).

This model produces recruitments that are log-normally distributed, and a correction factor of $\frac{\sigma^2}{2}$ is applied to $R_{(t)}$. The correction factor is included because it is commonly used in stock assessments. The Beverton-Holt stock recruitment relationship can be reparametrized as (Mace and Doonan[4])

$$\alpha = \frac{N_0}{R_0}\frac{1-h}{4h} \quad (2)$$

and

$$\beta = \frac{5h-1}{4hR_0}, \quad (3)$$

where N_0 = virgin abundance at equilibrium;
R_0 = virgin recruitment; and
h = recruitment steepness.

At equilibrium,

$$N_0 = N_0e^{-M} + R_0 \quad (4)$$

and

$$R_0 = DN_0, \quad (5)$$

where D = death rate and is equal to $1 - e^{-M}$.

We now introduce the persistence criterion. For a given h, the persistence criterion is defined as

$$p(n,t\,|\,h,T) = \Pr\left\{N_{(s)} > N_c \text{ for all } t \le s \le T \,|\, N_{(t)} = n\right\}, \quad (6)$$

where T = a time far into the future;
n = a specific value of population size; and
N_c = a critically low level of abundance, below which the population would have very high probability of extinction.

At $t = T$, $p(n,T|h,T) = 1$ if $n > N_c$ and $p(n,T|h,T) = 0$ otherwise. In addition, $p(n,t|h,T)$ satisfies the boundary condition that $p(N_c,t|h,T) = 0$ for all t.

For times previous to T, $p(n,t|h,T)$ satisfies the stochastic iteration equation (Mangel and Clark, 1988; Clark and Mangel, 2000)

$$p(n,t\,|\,h,T) = E_{R_t}\left\{p\left(ne^{-M} + \frac{n}{\alpha(h)+\beta(h)n}e^{R_t}, t+1\,|\,h,T\right)\right\}, \quad (7)$$

where E_{R_t} denotes the expectation over the stochastic processes associated with recruitment. We have indicated that the Beverton-Holt parameters depend upon steepness (as Eqs. 2–5 show, they also depend upon mortality M, which we hold to be a fixed value).

Because the recruitment uncertainty is normally distributed and Equation 7 cannot be evaluated analytically, we used a discrete distribution for R_t ($=R_{(t)}-\frac{\sigma^2}{2}$) into K (=61) uniformly spaced values (r_k) between -3σ and 3σ, so that

$$\Pr\{R_t = r_k\} = \frac{\exp\left(-\frac{r_k^2}{2\sigma^2}\right)}{\sum_{j=1}^{K}\exp\left(-\frac{r_j^2}{2\sigma^2}\right)}. \quad (8)$$

The iteration equation then becomes

$$p(n,t\,|\,h,T) = \sum_{k=-3\sigma}^{k=3\sigma}\Pr\{R_t = r_k\}\left\{p\left(ne^{-M} + \frac{n}{\alpha(h)+\beta(h)n}e^{r_k}, t+1\,|\,h,T\right)\right\}. \quad (9)$$

We solve Equation 9 backwards in time, starting at $t = T–1$ (Mangel and Clark, 1988; Clark and Mangel, 2000) until reaching $t = 1$. Assuming that the population starts at the deterministic steady state ($n=N_0$), we can then calculate the prior probability for each h value using Equation 9. Because h is bounded between 0.2 and 1, we used an interval of 0.005 so that a total of 161 solutions of Equation 9 are needed to produce the prior probability for h. We then used a logistic equation to fit 161 prior probability values to produce a derived h prior curve {$\phi(h)$}:

$$\phi(h) = \frac{\theta_1}{1+\frac{(\theta_1-\theta_2)}{\theta_2}e^{-\theta_3 h_1}}, \quad (10)$$

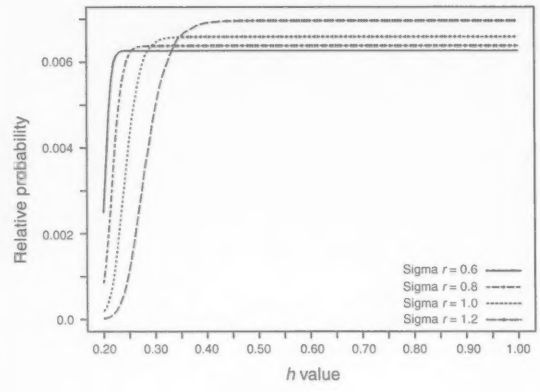

Figure 1

Relative probability distributions of the steepness (h) prior for four different σ values with the parameter setting M = 0.15, $N_c = 0.1N_0$, and T = 500 years.

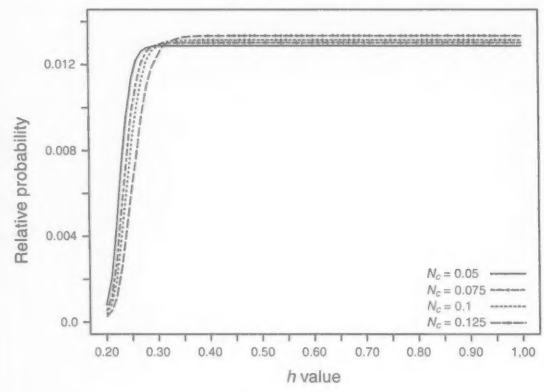

Figure 2

Relative probability distributions of the steepness (h) prior for four different N_c values with the parameter setting M = 0.15, σ = 1.0, and T = 500 years.

where $$h_1 = \frac{h - 0.2}{0.8} \quad (11)$$

and θ_1, θ_2, and θ_3 are parameters for a logistic equation.

Note that the derived h priors produced above are relative probabilities, but that is what is needed for the assessment models and Bayesian priors.

Results

Derived h prior curves for M = 0.15, $N_c = 0.1N_0$, and T = 500 years at four different values of recruitment variability (σ) are shown in Figure 1. In general, the prior probability of h increased rapidly at low h values, and then remained at constant values at high h values. As expected, when recruitment variability (σ) increased, h values were higher to compensate for higher recruitment variability (Fig. 1). Table 1 shows parameter values of logistic curves fitted to derived h prior distributions as natural mortality (M) ranged from 0.05 to 0.7 and recruitment variability (σ) ranged from 0.2 to 1.6. These fitted curves would be convenient to use in stock assessment models for given natural mortality and recruitment variability, and values can be interpolated for intermediate cases. Derived h prior curves for four N_c values were plotted (Fig. 2). The figure shows patterns similar to those for recruitment variability, namely that as N_c values increase, h values are higher to increase recruitment potential for the population. Derived h prior curves for four natural mortality (M) values (M=0.1, 0.15, 0.3, and 0.5, respectively) are shown in Figure 3. As M values increase, h values also increase.

Discussion

This article presents a simple modeling approach that allows one to use life history criteria to derive steepness priors for a fish stock where no sufficient historical data could be used to establish reasonable stock recruitment relationships. The model used in this article requires a few assumptions, most of which could be inferred from the life history of the species. However, there is a shortcoming in our approach: a simple population model is used to derive h priors and then applied to the stock assessment model that is an age-structured population model. To derive h priors by using age-structured models would require some age-specific parameters, such as fecundity, growth, and possibly age-specific natural mortality rates. That is, "prior" information on these parameters for age-structured models is needed but in many cases they are not readily available (if they were, the entire stock assessment would be much easier). The parameters for age-structured models could be borrowed from stock assessment models, but applying priors back to stock assessment models could be deemed to be "double" uses of data (Minte-Vera et al., 2005). Our simple population model approach has been widely used in many other applications, such as in computing extinction risk in conservation biology (Hakoyama et al., 2000) and in simple production models in fisheries assessments (MacCall, 2002). In these applications, simple (non–age-structured) models were used for populations that are known to have age- or size-structures.

Although there are only a few parameters needed for the model, there are uncertainties in choosing ranges of values for each parameter. One of the important parameters in determining the priors is N_c, the parameter

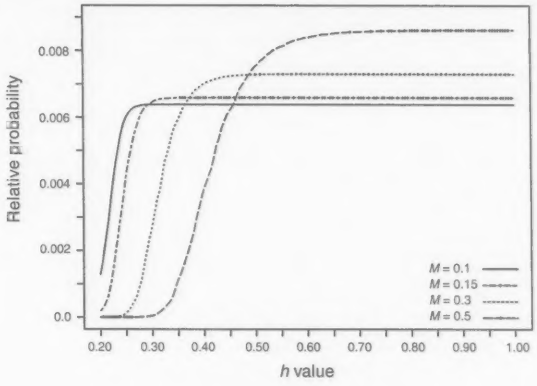

Figure 3

Relative probability distributions of the steepness (h) prior for four different natural mortality (M) values with parameter setting σ = 1.0, $N_c = 0.1N_0$, and T = 500 years.

characterizing critical abundance. This parameter is more or less a theoretical concept that defines the lowest population abundance deemed to be viable, and its value interacts with the time horizon, T. Although we used a relatively large value of N_c, the associated time horizon was short (T=500 yr) in the evolutionary time scale. Because the stock-recruitment dynamics near the origin are nearly linear, a relatively large value of N_c is approximately equivalent to using a lower value of N_c over a longer time horizon. Also, Mangel and Clark (1988) showed that once the time horizon is sufficiently large, the distributions have the same shape and become stationary. Test runs on our models with large values of T (T=3000 yr) showed almost the same results. In a complex marine environment like that of the U.S. west coast, it would be very difficult to determine "true" values of N_c and T, which could be, for example, at a level where the Allee effect is likely to take place and over a time scale of major environmental change, respectively. However, the results indicated that the model is not very sensitive to the N_c values (Fig. 2). For a range of N_c/N_0 values from 0.05 to 0.125, the prior probability curves were very similar. In contrast, recruitment variability (σ) had much greater effects on the distributions of the prior probability (Fig. 1). As recruitment variability increases, minimum h values need to be significantly higher in order to ensure population viability. Stock assessment reports on other west coast groundfish species have indicated a very high recruitment variability in the past few decades, such as for bocaccio, (σ=1.0, MacCall[2]), and darkblotched rockfish, (σ=0.85, Rogers[3]). However, some recent stock assessment models for the west coast groundfish species have used a lower value of σ, such as 0.6 (Punt, 2003). In our example, if lower values of σ are used, the derived h prior curves will be very flat for h>0.23 (Fig. 2), indicating that the population would be sustainable with very low h values.

Other methods for deriving h priors include using expert opinion, borrowing values from other taxonomically or ecologically related species, and using regional meta-analysis (Myers, 1998, 2001; Chen and Holtby, 2002; Dorn, 2002; Millar, 2002; Myers et al., 2002). For example, Myers et al. (2002) used an empirical Bayesian approach to derive prior distributions for steepness for nine species. As compared to our method, their method, based on a combined method of taxonomic and ecological criteria, still requires the collection of biological data from related species, as well as expert opinions on the life history of each species, which are somewhat "subjective" values. Dorn (2002) used Bayesian meta-analysis to derive stock-recruitment relationships for a group of west coast groundfish species. He used the results from the previous stock assessments for widow rockfish and other west-coast groundfish species and indicated that the prior distribution for steepness for widow rockfish could have a median value around 0.72 and a probability of 0.0033 for $h \leq 0.225$. This result could indicate that our method is more conservative because our method indicates much lower median value for widow rockfish-like species. Minte-Vera et al. (2005) also suggested that the priors derived by Dorn (2002) might not be appropriate for stock assessments that include the same data that were used in the meta-analysis to derive priors.

We believe that the method used in our study provides a scientific way of estimating the prior for steepness and avoids the pitfall of imposing a preconception of what the true distribution is thought to be. For example, it seems reasonable that very high values of h will not be likely because of tradeoffs between individual survival

Table 1

Parameter values of logistic curves fitted to derived h prior distributions for different natural mortality (M) and recruitment variability (σ). Parameters are listed in the order of θ_1, θ_2, and θ_3 (see Eq. 10). For some combinations of natural mortality and recruitment variability, distributions were uniform or could not be fitted.

Recruitment variability	Natural mortality									
	0.05	0.1	0.15	0.2	0.25	0.3	0.4	0.5	0.6	0.7
0.2	Uniform distribution	Uniform distribution	Uniform distribution	Uniform distribution	Uniform distribution	1.0000 669.60 0.9289	1.0000 443.00 0.8046	1.0000 306.13 0.6662	1.0000 282.66 0.5015	1.0000 278.16 0.3724
0.4	Uniform distribution	0.9994 139.90 0.9800	1.0000 248.40 0.7973	1.0000 223.60 0.5585	1.0000 196.43 0.3739	1.0000 199.3 0.2146	0.9999 182.22 0.08619	0.9999 157.82 0.04454	0.9999 148.63 0.02264	0.9997 145.48 0.01154
0.6	Uniform distribution	1.0000 149.70 0.7552	1.0000 133.60 0.3895	1.0000 116.74 0.1791	0.9998 109.86 0.08069	0.9995 105.32 0.03805	0.9992 89.55 0.01543	0.9988 78.79 0.007602	0.9985 69.29 0.005074	 61.48 0.003861
0.8	1.0000 83.00 0.9259	1.0000 93.13 0.4317	1.0000 84.25 0.1376	0.9997 76.29 0.04540	0.9992 68.73 0.02022	0.9990 65.53 0.01197	0.9982 48.84 0.005796	0.9972 40.51 0.003745	0.9959 34.03 0.003041	0.9943 29.12 0.002722
1.0	1.0000 75.30 0.9526	1.0000 64.42 0.1929	0.9995 57.52 0.04464	0.9987 48.77 0.1700	0.9980 41.44 0.009240	0.9970 35.57 0.006199	0.9944 27.15 0.003906	0.9902 21.58 0.003076	0.9830 17.71 0.002680	0.9709 14.97 0.002402
1.2	1.0000 69.36 0.5920	0.9995 48.16 0.07182	0.9983 38.71 0.01844	0.9967 30.90 0.009036	0.9946 25.38 0.005819	0.9915 21.26 0.004420	0.9801 15.75 0.003134	0.9543 12.64 0.002243	0.9011 11.01 0.001320	0.8085 10.34 0.0005882
1.4	1.0000 47.79 0.2024	0.9983 35.06 0.02504	0.9956 25.81 0.009163	0.9913 19.87 0.005647	0.9835 15.94 0.004010	0.9697 13.39 0.003087	0.9025 10.74 0.001373	0.7428 10.25 0.0003183	0.4973 10.88 0.00003683	0.2428 12.62 0.0000016
1.6	0.9992 39.09 0.03001	0.9955 25.03 0.008900	0.9883 17.22 0.004923	0.9716 13.22 0.003340	0.9338 11.08 0.001971	0.8585 10.25 0.0008686	0.5463 10.75 0.00005315	0.2027 12.90 0.00000079	0.02790 16.85 0.00000001	Not fitted

and reproduction, but that tradeoff should be shown, not imposed. The methods used in the present study can be extended to address this tradeoff (i.e., Mangel and Clark, 1988; Clark and Mangel, 2000), but that is a subject for another study. However, for many overfished stocks that need stock-recruitment relationships for rebuilding analysis, this method is especially appropriate because it indicates the ability of the population to recover from low abundance. For other depleted stocks, use of prior probability distributions based on this method can provide useful information on how quickly the populations could be rebuilt under various management policies.

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Survival of white marlin (*Tetrapturus albidus*) released from commercial pelagic longline gear in the western North Atlantic*

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Abstract—To estimate postrelease survival of white marlin (*Tetrapturus albidus*) caught incidentally in regular commercial pelagic longline fishing operations targeting swordfish and tunas, short-duration pop-up satellite archival tags (PSATs) were deployed on captured animals for periods of 5–43 days. Twenty (71.4%) of 28 tags transmitted data at the preprogrammed time, including one tag that separated from the fish shortly after release and was omitted from subsequent analyses. Transmitted data from 17 of 19 tags were consistent with survival of those animals for the duration of the tag deployment. Postrelease survival estimates ranged from 63.0% (assuming all nontransmitting tags were evidence of mortality) to 89.5% (excluding nontransmitting tags from the analysis). These results indicate that white marlin can survive the trauma resulting from interaction with pelagic longline gear, and indicate that current domestic and international management measures requiring the release of live white marlin from this fishery will reduce fishing mortality on the Atlantic-wide stock.

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White marlin (*Tetrapturus albidus* Poey 1860) is an istiophorid billfish species widely distributed in tropical and temperate waters throughout the Atlantic Ocean, including the Caribbean Sea. There is substantial international concern regarding the population levels of this species. The standing committee for research and statistics (SCRS) of the International Commission for the Conservation of Atlantic Tunas (ICCAT) last assessed the Atlantic-wide stock of white marlin in 2002 and in its continuity-case assessment the committee indicated a total biomass of approximately 12% of that necessary to produce maximum sustainable yield. It was also estimated that the current international fishing mortality level for this species is equivalent to more than eight times the replacement yield, contributing to further decline of the overfished stock (ICCAT, 2005).

Both recreational and commercial fisheries contribute to the mortality of white marlin. A directed recreational fishery exists throughout the tropical and temperate Atlantic (with considerable effort off the coasts of Brazil and Venezuela), as well as off the U.S. mid-Atlantic coast, and there is a growing trend towards catch-and-release practices in all directed recreational billfish fisheries. In contrast to the catches by this directed recreational effort, white marlin are an infrequent bycatch or a retained incidental catch of the international pelagic longline fishery, which targets tunas (*Thunnus* spp.) and swordfish (*Xiphias gladius*). Although white marlin catches in the pelagic longline fishery are relatively rare, the fishery accounts for the majority of the total fishing mortality on this species simply because of the sheer magnitude of pelagic longline effort exerted throughout the Atlantic (ICCAT, 2005).

Both domestic and international management measures are currently in effect for white marlin. The U.S. recreational fishery is managed with a 66″ lower jaw-fork length federal minimum size and a binding ICCAT recommendation that limits the annual U.S. recreational landings to a total of 250 blue marlin (*Makaira nigricans*) and white marlin combined (ICCAT, 2000). U.S. commercial fishermen have been prohibited from landing or possessing white marlin since the implementation of the National Marine Fisheries Service (NMFS) Fishery Management Plan for Atlantic Billfish (NMFS, 1988). ICCAT has responded twice to the decreasing biomass of white marlin and blue marlin by adopting binding

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recommendations requiring reductions in commercial landings by both pelagic longline and purse seine gears (ICCAT, 2000, 2001a). However, these reductions in landings by themselves may ultimately be insufficient to rebuild these two marlin stocks. Goodyear (2002a) found that a reduction of 60% would be necessary to halt the decline of blue marlin, a species which is more abundant, larger, and presumably more robust to the trauma associated with commercial capture (Kerstetter et al., 2003). Given that white marlin are smaller animals, and that the stock is more depleted than that of blue marlin, even more drastic measures are likely necessary to achieve the same management goal for this species.

Because the pelagic longline fishery accounts for the majority of white marlin mortality, understanding the nature of billfish interactions with this gear is critical to developing effective strategies to reduce fishing mortality. Jackson and Farber (1998) reported that 56% of white marlin caught in the Venezuelan longline fishery between 1987 and 1995 were alive at the time of haulback. Data from the U.S. observer program and mandatory pelagic longline logbook records indicate that 71% of white marlin were released alive from U.S. commercial pelagic longline gear between 1996 and 1998 (Cramer[1]). ICCAT has long been encouraging the release of live white marlin through both binding and nonbinding resolutions (ICCAT, 1995, 1996). More recently, the commission has approved binding recommendations that require the release of all live white marlin caught by purse seine and pelagic longline vessels (ICCAT, 1997, 2001b). However, those animals released alive must have a reasonable probability of survival for such management measures to be ultimately effective.

The assessment of postrelease survival presents special problems for large pelagic fishes, which are rarely capable of being held in captivity (de Sylva et al., 2000). In general, recovery rates of billfish tagged with conventional streamer tags by commercial and recreational fishermen have been quite low (0.4–1.83%: Prince et al., 2003; Ortiz et al., 2003). Although this observation is consistent with high postrelease mortality, low recovery rates could also result from tag shedding and from tags that fail to transmit data (Bayley and Prince, 1994; Jones and Prince, 1998). The results of acoustic tracking studies of various billfish species (e.g., striped marlin [*Tetrapturus audax*]: Brill et al., 1993; blue marlin: Block et al., 1992; and black marlin [*Makaira indica*]: Pepperell and Davis, 1999) captured on recreational gear indicate that postrelease survival over periods of a few hours to a few days is relatively high, although mortalities have been observed in short-term tracking studies. Recently, pop-up satellite archival tag (PSAT) technology has proven especially useful to study postrelease survival in several larger istiophorid species, including blue marlin in the Atlantic (Graves et al., 2002; Kerstetter et al., 2003) and striped marlin in the Pacific (Domeier et al., 2003). Only recently have PSATs been attached to smaller (<40 kg) istiophorid billfishes. Horodysky and Graves (2005) used PSATs to evaluate the postrelease survival of white marlin from recreational (rod-and-reel) fishing gear and demonstrated that smaller billfish (≥16 kg estimated weight) can carry PSATs. Their work also suggested high postrelease survival rates in the recreational fishery, especially for fish caught on circle hooks. However, pelagic longline gear presents a different suite of stressors during capture of an animal than does recreational gear. These differences, including long "soak times" (the length of time in each deployment of the gear that the longline is fishing), may also affect postrelease survival rates. In our study, we applied PSAT technology to estimate the short-term mortality of white marlin released alive after capture on pelagic longline gear.

Materials and methods

Fishing operations

White marlin tagging took place off the east coast of Florida (FL), the southwest edge of Georges Bank (GB), the Yucatan Channel (YC), the Windward Passage (WP), and the Mid-Atlantic Bight (MA). These locations are all waters traditionally fished by the U.S. pelagic longline fleet. All tagging operations occurred opportunistically aboard the commercial pelagic longline fishing vessel FV *Carol Ann* (54′ length-over-all) between June 2002 and August 2004. This vessel is typical in size and is equipped for targeting swordfish, mixed swordfish, and tuna within the U.S. coastal pelagic longline fishery. Hook types and sizes were also typical for the fishery and included 7/0 and 9/0 offset J-style hooks (ca. 15º offset; Eagle Claw model no. 9016 or Mustad model no. 7698), 16/0 non-offset circle hooks (Mustad models no. 39660 or no. 39666), and 18/0 non-offset circle hooks (Lindgren-Pitman, Inc., Pompano Beach, FL). Adjusted seasonally, individual leader lengths were 7.5 fathoms (ca. 13.7 m) in the fall northern fishery targeting tuna and 15 fathoms (ca. 27.4 m) in the spring southern fishery for swordfish; this adjustment is standard practice within the fleet (O'Neill[2]). Individual leader lengths comprised a two-fathom "tail" separated from the rest of the leader by a 28-g leaded swivel—a configuration commonly used in this fishery to reduce tangles with other leaders or the mainline. Varying the length of the lines ("buoy drops") connecting the mainline with the small buoy floats on the surface also allows the gear to fish at different depths. Many captains will use two buoy drop lengths in the beginning of a trip to ascertain

[1] Cramer, J. 2000. Species reported caught in the U.S. commercial pelagic longline and gillnet fisheries from 1996–1998. NMFS Sustainable Fisheries Division publication, SFD-99/00-78:1–33. NOAA/NMFS Southeast Fisheries Science Center, SFD, 75 Virginia Beach Dr., Miami, FL 33149.

[2] O'Neill, G. 2003. Personal commun. Carol Ann Sword Corporation. 629 NE 3rd Street, Dania Beach, FL 33004.

the most productive gear configuration. For our study, two buoy drop lengths were used in each set, and these drop lengths were alternated after every 30 hooks: usually 5- and 2.5-fathom (ca. 9.1 and 4.5 m, respectively) lengths in the fall and 10- and 12-fathom (ca. 18.3 and 21.9 m, respectively) lengths in the spring. Electronic hook-timers (Lindgren-Pitman, Inc.; Pompano Beach, FL) were also used during many of the sets to record the time at which an animal was hooked. Bait was usually frozen squid (*Illex* sp.), but occasionally included frozen Atlantic mackerel (*Scomber scombrus*) or a haphazard mixture of the two.

This project consisted of both a pilot and a main study. The pilot study occurred off the east coast of Florida during June 2002 and included deployments of five PTT-100 tags (Microwave Telemetry, Inc.; Columbia, MD) and one PAT (Wildlife Computers; Redmond, WA) tag. The main study was conducted between August 2002 and August 2004 and for this study only PTT-100 HR model tags were used.

Tag models

The physical characteristics of all PSAT tag models used in this study were similar and included a microprocessor, a transmitter, and various environmental sensors, all contained within a resin-filled carbon fiber tube. The tag is made positively buoyant by a spherical glass-bead–embedded float at the base of the antenna. It measures approximately 38 cm in length by 4 cm diameter (including antenna) and weighs between 65 and 75 g (air weight). Tags were rigged with approximately 16 cm of 400-pound test Momoi® brand (Momoi Fishing Co.; Ako City, Japan) monofilament line attached to a large hydroscopic nylon intramuscular tag head according to the method of Graves et al. (2002). The earlier model PTT-100 tags were identical to those used by Graves et al. (2002) and Kerstetter et al. (2003) and recorded one temperature data point for every two-hour period during their five-day (n=3) or 30-day (n=2) deployments, as well as a pre- and postdeployment inclinometer value. The PAT tag recorded environmental data every minute during its 43-day deployment (programmed to disengage from the fish on 30 July 2002) but transmitted data as summary histograms rather than discrete data points. The PAT tag possessed emergency release software as well as a mechanical device (RD-1500; Wildlife Computers, Redmond, WA) for an early emergency release before reaching a depth at which it would be crushed by ambient water pressure (crush depth).

The Microwave Telemetry, Inc. model PTT-100 HR satellite tag was used for the main study and constituted the majority of the PSAT deployments (n=22). This tag has similar physical attributes to those of the model PTT-100 tags previously described, but its functionality was increased by the addition of light and pressure (depth) sensors and an increased data storage capacity. The manufacturer preprogrammed all the PTT-100 HR model tags to detach themselves from the fish after ten days, and the tags were activated prior to attachment to the animal by removing a small magnet from the side of the tag. The tags sampled environmental data at approximately four-minute or two-minute intervals.

White marlin tagging procedures

Preparations for tagging operations were made before each haulback of the gear. Tags were either activated prior to haulback or during haulback immediately following the tagging of a fish and during preparation for tagging another animal. Regardless of the time of external tag activation, all PSATs were allowed to cycle through their full ten-minute computerized internal activation process prior to being attached to a fish. The captain of the vessel identified incoming white marlin on the line during the morning haulback of the gear and fish were evaluated as live or dead based on movement (or lack thereof) alongside the vessel. All live white marlin were tagged, regardless of physical condition.

Fish were manually brought alongside the vessel just aft of the hauling station along the rail and held briefly by the leader until calm. The average distance between the top of the rail and the fish (free-board) on the FV *Carol Ann* was approximately one meter, requiring the use of a tagging pole of approximately 2 m length to reach the fish over the gunwale. The nylon anchor to the PSAT tether was carefully inserted about 5–10 cm below the midpoint of the anterior dorsal fin to a depth of about 5 cm. This location on the fish provides an opportunity for the nylon tag head to pass through the pterygiophore bones without approaching the coelemic cavity (Prince et al., 2002a). For most white marlin in this study (93%), a conventional streamer tag was also attached well posterior to the PSAT.

White marlin were released as soon as possible after tagging by the standard commercial protocol of cutting the leader near the hook unless the hook was readily accessible for manual removal. No animals were resuscitated after tagging. Prior to release, hook type was noted and fish lengths and weights were estimated. Disposition ("live" vs. "dead") and hook location data were collected for all white marlin caught in 2003 and 2004. For the purposes of this study, "internal" hook locations were those in which the barb of the hook was lodged posterior to the esophageal sphincter, and "external" hook locations were noted with more specificity (e.g., "upper jaw"). Hooking on the body away from the mouth ("foul hooking") was considered an "external" hook location. In addition to noting hooking location, a rapid visual examination of each fish was conducted using the five-point "ACESS" scale of activity, color, eye condition, stomach status, and body state (see Kerstetter et al., 2003). The tagging operation, from positive species identification to actual release from the gear, lasted less than 10 minutes. All data, including the time of day, vessel location, and surface water temperature, were recorded immediately after tagging.

Table 1

Summary of locations, trips, and individual sets taken on a commercial pelagic longline vessel between June 2002 and August 2004 during tagging activities. Location refers to National Marine Fisheries Service (NOAA) statistical areas: FEC = Florida East Coast, NEC = Northeast Coastal, MAB = Mid-Atlantic Bight, GOM = Gulf of Mexico, and CAR = Caribbean. For hook type, OS = offset and NOS = non-offset.

	2002		2003	2004	
Months	June	August	July–September	January–February	August
Location	FEC	NEC	MAB	GOM and CAR	MAB
Number tagged	6	2	6	2	12
Sets with tagging	5	1	5	2	3
Bait type	frozen squid	frozen squid	frozen squid	frozen squid, frozen mackerel, or mixture	frozen squid, frozen mackerel, or mixture
Hook type	OS 9/0 J-style and NOS 18/0 circle	OS 9/0 J-style and NOS 16/0 circle	OS 9/0 J-style and NOS 16/0 circle	OS 9/0 J-style and NOS 16/0 circle	NOS 16/0 circle

Data analysis

Survival of tagged animals was inferred from three types of environmental data provided by the tag: water temperature changes, depth changes, and ambient light intensity. Frequent short-scale (<1 hour) variations in both depth and temperature were used as indicators of a live white marlin. The survival of individual fish was also supported by the net displacement, calculated as the distance from the location of the vessel at the time the white marlin was released to that of the first good transmission from the free-floating PSAT to the ARGOS satellite system. The precision of reported location estimates was based on the attitude of the receiving satellite, and transmissions were generated through the ARGOS system (Service Argos, Inc., Largo, MD) and categorized into seven location accuracy codes. Locations were considered "good" for our study if the ARGOS system reported an accuracy code that corresponded to a distance of less than 1000 meters. If a good position was not obtained directly from ARGOS, an average of all location code "0" readings from the first 24-hour period of transmission was used as a proxy location. All distances were calculated with PROGRAM INVERSE (NGS[3]).

Estimates of white marlin postrelease survival were calculated both by including nontransmitting tags as evidence of mortalities and by excluding nontransmitting tags. The 95% confidence intervals associated with these estimates were calculated by using the RELEASE MORTALITY version 1.1.0 software developed by Goodyear (2002b). These confidence intervals were based on 10,000 simulations where underlying postrelease mortality rates derived from the transmitted data were assumed to have no error sources (e.g., no premature releases or tag-induced mortality). For the purpose of these simulations, natural mortality was also assumed to be zero because of the relatively short duration of the tagging deployment period. Unless otherwise noted, all statistical analyses for this study were conducted with SAS version 8.3 (SAS Institute, Cary, NC).

Results

Eight trips (n=112 sets) were taken between June 2002 and August 2004 on the FV *Carol Ann*, a U.S.-registered commercial pelagic longline vessel that operated during the winter and spring in the Caribbean Sea targeting swordfish and during the summer and fall in the mid-Atlantic and Georges Bank region targeting both tuna and swordfish. A summary of these trips and sets is provided in Table 1. Sets were typically made overnight, and gear was deployed at dusk and retrieved at dawn.

Catch rates (catch per 1000 hooks) for target and bycatch species varied by season and location. Swordfish catch rates for retained animals ranged from 1.6 (mid-Atlantic, summer 2005) to 23.9 (Caribbean and Gulf of Mexico, spring 2004). Retained tuna (yellowfin [*Thunnus albacares*]; bigeye, *T. obesus*; and albacore [*T. alalunga*]) catch rates ranged from 0.8 (Caribbean and Gulf of Mexico, spring 2004) to 44.2 (mid-Atlantic, summer 2004). Istiophorid billfishes (blue marlin, white marlin, longbill spearfish [*Tetrapturus pfluegeri*], and sailfish [*Istiophorus platypterus*]) represented approximately 3% of the catch by number, and the overall mean catch rate of white marlin was 1.87 per 1000 hooks. Proportions of white marlin dead at the time of haulback varied among sets, trips, seasons, and locations. The lowest observed proportion dead was 34.4% (mid-Atlantic, summer 2005) and the highest was 50%

[3] NGS (National Geological Survey). 1975. Version 2.0, modified by M. Ortiz, NOAA/NMFS Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, FL 33149.

Table 2

Summary information for tagged white marlin (*Tetrapturus albidus*) released from commercial pelagic longline gear in the western North Atlantic Ocean, June 2002–August 2004. "D/NV" refers to hooks that were deep and not externally visible at the time of tagging. Y=yes; No=no. L=live; PR=premature release; D=dead. —=not available. MSLD=minimum straight line distance (distance between the point where the animal was released and the area where the tag began transmitting data.)

Tag number	Deployment duration	Tag model	Hook type	Hook location	Estimated weight (kg)	Report?	Fate?	% Data	MSLD (nmi/km)
FL-02-01	5-day	PTT-100	18/0 circle	eye socket	18	Y	L	100	42/78
FL-02-02	5-day	PTT-100	9/0 J-style	jaw	27	N	—	—	—
FL-02-03	5-day	PTT-100	9/0 J-style	jaw	20	Y	L	100	26/48
FL-02-04	30-day	PTT-100	18/0 circle	foul	18	Y	PR	n/a	—
FL-02-05	30-day	PTT-100	9/0 J-style	roof	20	N	—	—	—
FL-02-06	43-day	PAT	18/0 circle	eye socket	16	Y	L	33.4	806/1493
GB-02-01	10-day	PTT-100 HR	7/0 J-style	D/NV	20	Y	D	81.5	—
GB-02-02	10-day	PTT-100 HR	16/0 circle	eye socket	23	Y	L	100	109/202
MA-03-01	10-day	PTT-100 HR	9/0 J-style	D/NV	23	N	—	—	—
MA-03-02	10-day	PTT-100 HR	9/0 J-style	eye socket	25	Y	L	85.1	136/252
MA-03-03	10-day	PTT-100 HR	9/0 J-style	jaw	20	Y	L	67.5	80/149
MA-03-04	10-day	PTT-100 HR	16/0 circle	jaw	25	Y	D	57.3	—
MA-03-05	10-day	PTT-100 HR	9/0 J-style	roof	23	N	—	—	—
MA-03-06	10-day	PTT-100 HR	9/0 J-style	roof	25	Y	L	86.1	161/298
YC-04-01	10-day	PTT-100 HR	16/0 circle	jaw	16	N	—	—	—
WP-04-01	10-day	PTT-100 HR	16/0 circle	corner	23	Y	L	100	60/110
MA-04-01	10-day	PTT-100 HR	16/0 circle	eye socket	20	Y	L	44.1	525/973
MA-04-02	10-day	PTT-100 HR	16/0 circle	D/NV	20	N	—	—	—
MA-04-03	10-day	PTT-100 HR	16/0 circle	eye	16	Y	L	16.4	301/557
MA-04-04	10-day	PTT-100 HR	16/0 circle	eye socket	25	Y	L	70.5	632/1170
MA-04-05	10-day	PTT-100 HR	16/0 circle	eye	25	N	—	—	—
MA-04-06	10-day	PTT-100 HR	16/0 circle	eye socket	23	Y	L	22.8	332/615
MA-04-07	10-day	PTT-100 HR	16/0 circle	D/NV	18	N	—	—	—
MA-04-08	10-day	PTT-100 HR	16/0 circle	jaw	14	Y	L	4.4	81/149
MA-04-09	10-day	PTT-100 HR	16/0 circle	jaw	20	Y	L	48.3	436/807
MA-04-10	10-day	PTT-100 HR	16/0 circle	jaw	20	Y	L	17.6	250/463
MA-04-11	10-day	PTT-100 HR	16/0 circle	jaw	23	Y	L	51.0	89/164
MA-04-12	10-day	PTT-100 HR	16/0 circle	jaw	27	Y	L	18.8	255/473

(Caribbean and Gulf of Mexico, spring 2004). The average proportion of white marlin dead at haulback across all seasons and trips was 35.4%.

PSATs were applied to 28 white marlin at the time of haulback. All live white marlin brought to the vessel were tagged regardless of physical condition until the supply of tags available on that trip was exhausted (i.e., if a fish was evaluated as being alive, it was tagged). Estimated weights of tagged fish ranged from 14–27 kg (30–60 pounds) and detailed information for each individual tagged (including hook location, fate, and minimum straight-line distance) is presented in Table 2. Three white marlin tagged with PSATs were caught on leaders attached to electronic hook-time recorders, allowing us to determine the length of time the animal was on the hook before release. Two fish (YC-04-01 and WP-0401) struck the bait in the early morning after local sunrise (7:32 and 8:13 a.m. local time, respectively) and were on the line only for approximately 1.5 hours before release. The third fish (MA-03-01) was caught during haulback at 9:52 p.m. local time on one of the few sets retrieved at night and was hooked for only 11 minutes.

Tag performance

In the pilot study, four of six tags (67%) transmitted archived data as programmed. One tag separated from the fish prematurely several hours after deployment and the data from this tag were omitted from subsequent analyses. For each of the three transmitting early model PTT-100 tags, 100% of the 63 archived data points were received, whereas approximately 33% of the summary data were received from the PAT tag. In the main study,

16 (72.7%) of the 22 PTT-100 HR tags transmitted data to satellites in the ARGOS system as programmed, and an average of 51% (range 4.4–86.1%) of each tag's archived data were transmitted. Two PTT-100 HR tags were found on shore after their transmission period and were returned to us and all the archived data were recovered from each tag.

White marlin survival

Transmitted temperature and depth data from 17 of the 19 functional tags (89.5%) indicated that released white marlin survived for the time periods over which the tags were programmed to collect data. Of the two confirmed mortalities in this study, one fish (GB-02-01) died within one hour after release and sank to the bottom at 145 meters depth. It remained there for approximately 10 hours before the tag and presumably the carcass were scavenged by a shark based on an abrupt change in behavior (depth distribution and movements) and light level (see Kerstetter et al., 2004). The second mortality (MA-03-04) occurred approximately 24 hours following release. After tagging, the animal remained between 0 and 26.9 meters depth before it too was inferred to be the victim of a shark predation event based on similar changes in environmental parameters.

The net displacement of all reporting tags was used as an additional line of evidence to assess postrelease survival of white marlin. All of the tags from putatively surviving animals demonstrated net movements that cannot be explained by surface currents alone. For the 14 surviving fish with PTT-100 HR tags, the average minimum straight-line movement was 246.2 nautical miles (nmi) over the ten-day period, but there was a wide range of net displacement among individuals (80.4–631.5 nmi). Eight of the nine white marlin tagged approximately 350 miles east of Ocean City, Maryland, in summer 2004 moved generally east to northeast, with the exception of one animal that traveled 304.9 nmi to the northwest.

All but one of the tags employed in this study lacked hardware or software that would cause the tag to separate from the fish prematurely if a moribund fish descended below a critical depth. Consequently, nontransmitting tags could result from an animal that died and sank in waters deeper than the pressure capacity of the tags. All eight white marlin tagged with PSATs that did not transmit data were released in or near areas with depths in excess of 2000 meters, the manufacturer's suggested pressure limit for the tags.

The tags that did not transmit data may or may not represented mortalities of the tagged white marlin. These resulting calculated mortality rates therefore depend on whether or not the tags that did not transmit data are included as evidence of mortality. Combining both hook types, the overall mortality rate was 10.5% (95% CI: 0.0–26.3%) if nontransmitting tags were excluded and 37.0% (95% CI: 18.5–55.6%) if nontransmitting tags were included as mortalities.

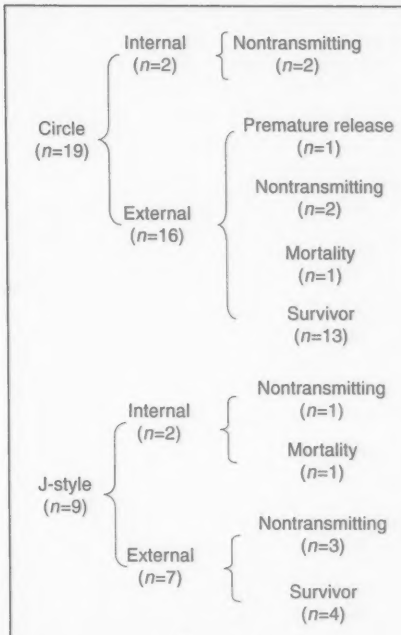

Figure 1

Fate of each white marlin (*Tetrapturus albidus*) tagged with PSAT tags and released from commercial pelagic longline gear in the western North Atlantic Ocean, June 2002–August 2004.

Hook performance

Two general hook types, circle and J-style, were used by the crew of the longline vessel in this study. Nineteen white marlin tagged with PSATs were caught on circle hooks, two of which (10.5%) were lodged internally and 17 of which (89.5%) were lodged externally in the jaw or mouth (Fig. 1). Neither of the two PSATs on animals hooked internally with circle hooks transmitted data. Two PSATs attached to the 17 fish caught with circle hooks lodged externally failed to transmit data, and only one fish caught with a circle hook lodged externally was a confirmed mortality. Nine white marlin tagged with PSATs were caught by J-style hooks. Two fish caught with J-style hooks were hooked internally (22.2%) and seven externally (77.8%). Of the two hooked internally, one tag did not transmit data and the other (fish GB-02-01) was a confirmed mortality. Three of the remaining seven tags on fish caught externally with J-style hooks did not transmit data. Comparisons of hook type and postrelease survival were not significant (Fisher's exact; $P>0.16$). For the 10° offset J-style hooks, the mortality rate was 20.0% excluding nontransmitting tags, and 55.6% if nontransmitting tags were included as mortalities. The 0° offset circle hooks had a 7.1% mortality rate if nontransmitting tags were excluded and 27.7% if

these nontransmitting tags were included as evidence of mortalities.

Nine white marlin were hooked in or near the eye. Seven fish were hooked on either circle or J-style hooks through the eye socket (with no visible damage to the eyeball) and all survived for the 5- or 10-day PSAT deployments. Two PSATs were attached to animals that had been hooked with a circle hook through the eye itself. One PSAT transmitted data consistent with survival, and the other tag did not transmit data. Only one white marlin tagged in this study was foul-hooked, caught in the ventral musculature by a size 18/0 circle hook. The PSAT attached to this fish separated from the fish prematurely.

Discussion

The amount of data archived and transmitted varied greatly among the three models of satellite tags, as well as among the 16 transmitting PTT-100 HRs. The early model PTT-100 tags archived only 63 data points, but 100% of the archived information was transmitted, providing sufficient information to infer survival (Graves et al., 2002; Kerstetter et al., 2003). In contrast, the newer PTT-100 HR tags archived either 4500 or 9145 data points, but not all archived data were transmitted. In this study, most of these tags transmitted a relatively large percentage of the archived data, facilitating determination of the fate of the released white marlin. However, one tag (MA-04-08) had an unusually low data transmitting rate of 4.4%, representing 315 data points over the ten-day tag deployment. Because these data points were transmitted in 11-minute blocks (approximately 9 data points each), they often included complete short-duration movements of a fish from the surface to depth. As the transmitted blocks of data were distributed haphazardly over the entire ten-day tagging period, it remained possible to determine postrelease survival from a high-resolution tag with a low data recovery rate.

Prior studies of postrelease survival have used different lengths of time to ascertain the effects of capture. These have included studies focused on postrelease survival as well as others addressing long-term behavior, movements, and habitat preferences. Graves et al. (2002) justified a five-day deployment period for blue marlin by citing reports of blue marlin recaptured within five days after being released with conventional tags from the recreational fishery, thus demonstrating a return to feeding. Kerstetter et al. (2003) adopted a similar position, although their study on blue marlin also included the deployments of two PSATs for 30 days to evaluate the possibility of delayed mortality. Domeier et al. (2003) used a variety of deployment periods (1–12 month durations) to assess postrelease survival in striped marlin. However, the longer the PSAT deployment period, the more susceptible the animal becomes to both fishing (i.e., recapture) and natural mortality, such as predation, biasing upwards the estimate of postrelease mortality (Goodyear, 2002b).

In our study, we primarily used tags with a ten-day deployment period and believe that this period is sufficiently long to document short-term mortality. Five of seven white marlin mortalities reported in Horodysky and Graves (2005) occurred within the first six hours of release, and the other two died less than three days later. All of the mortalities inferred for the closely related striped marlin by Domeier et al. (2003) occurred within six days of release, and 75% of these mortalities happened in less than two days. The two documented mortalities in the present study (GB-02-01 and MA-03-04) occurred within 24 hours of release.

Direct comparisons of estimates of postrelease survival of billfishes among previous acoustic and PSAT studies are problematic. Many acoustic tracking studies had relatively short observation periods and low sample sizes, and often fish in marginal physical condition were not tagged (reviewed in Domeier et al., 2003). Even among PSAT tagging studies, nontransmitting tags have been addressed with different protocols by various authors. Neither Graves et al. (2002) nor Kerstetter et al. (2003) directly observed mortalities of PSAT-tagged blue marlin. However, in both studies a conservative approach was adopted to estimate postrelease survival by considering nontransmitting tags as representing mortalities; this approach was adopted in part because of a lack of emergency release software or mechanisms on the tags themselves that would release the PSAT prior to its sinking with a dead fish below the depth at which the tag would be crushed. Some new models of satellite tags possess such emergency release software or physical mechanisms, such as glass implosion devices (Domeier et al., 2003) or the RD-1500 metal guillotine from Wildlife Computers (Redmond, WA) that sever the tether of the tag prior to reaching the depth limit of the tag. New generations of tags are also rated to greater crush depths (ca. 2000 m) than earlier models. The PSATs used in our study, with the exception of the one PAT tag, did not possess emergency release software or physical mechanisms. Because all the animals in this study were tagged over or near waters deeper than the crush depths of the tags, any deaths of tagged white marlin could have resulted in the PSATs being destroyed prior to transmitting data while the tag remained attached to the sinking, moribund fish.

There are several reasons why PSATs may not report even with emergency releases, including recovery of the tag by a noncooperative fishing vessel, internal malfunction, or biological activities. Kerstetter et al. (2004) reported on three PSAT tags that were presumably ingested by sharks during predation or scavenging and suggested that a number of nontransmitting tags in all PSAT studies could result from biological activity. Goodyear (2002b) noted that including nontransmitting tags as mortalities would bias mortality estimates upwards if the failure to transmit data was due to causes other than mortality.

The combination of physically more robust tags, emergency release capabilities, and demonstrated mortalities has led authors (e.g., Domeier et al., 2003) to specifi-

cally exclude tags that do not transmit data from subsequent analyses. Because it was not possible to estimate how many such tags in this study could have been due to malfunction versus individual mortality events, we chose to conservatively estimate two postrelease mortality rates: one that includes all nontransmitting tags as mortalities and another that excludes nontransmitting tags. The expensive nature of PSAT technology resulted in relatively small sample sizes and hence large confidence intervals for the estimated postrelease mortality rates. However, as with Horodysky and Graves (2005), simulations with the observed rates in the present study have shown that very large sample sizes (over 200 tags for each hook type) under ideal conditions would be required to reduce these estimates to within ±5% of the true value. The advent of newer tag models with features such as an emergency release will presumably result in lower nontransmitting rates for PSATs and hence more accurate estimates of postrelease survival.

In this study, PSATs attached to some white marlin in marginal physical condition at the time of release returned data consistent with postrelease survival. These included fish MA-04-03, which was hooked through the right eyeball, and fish WP-04-01, which displayed poor, faded color and was moving so little at haulback that it initially appeared dead until careful inspection. Both internal hooking and stomach eversion have been suggested as predictors of subsequent mortality for billfishes (Domeier et al., 2003). Horodysky and Graves (2005) found a 40% mortality rate for internally hooked white marlin, and Domeier et al. (2003) found a 63% mortality rate for similarly hooked striped marlin. We tagged four internally hooked animals, and the one reporting tag (GB-02-01) indicated mortality shortly after release for that fish. Three white marlin with everted stomachs at haulback were tagged in this study, but only one (MA-03-04) remained attached for the duration of the deployment period and transmitted data consistent with mortality. However, the survival of a white marlin (Horodysky and Graves, 2005) and a striped marlin (Holts and Bedford, 1990) with everted stomachs indicates that billfish with everted stomachs can survive if released.

White marlin captured with circle hooks demonstrated a trend of lower postrelease mortality than those hooked with J-style hooks, but this relationship was not significant. This trend in mortality rate versus hook type was independent of whether nontransmitting tags were included as mortalities or excluded from analyses. Horodysky and Graves (2005) observed a significant decrease in mortality for white marlin caught on circle hooks than on J-style hooks (0% versus 35% for J-style hooks). Domeier et al. (2003) also noted a trend for a lower mortality rate among animals hooked with non-offset circle hooks (12.5% versus 29.4% for offset J-style hooks), although this relationship was not significant. The lower mortality-rate trend for white marlin caught by circle hooks than by J-style hooks presented in the present study is also consistent with the results in several other studies of pelagic fishes, such Prince et al. (2002b) for recreationally caught billfish and Skomal et al. (2002) with recreationally caught Atlantic bluefin tuna (*Thunnus thynnus*), which based predictions of postrelease survival on likely injury resulting from specific hooking locations on the animals.

The majority of white marlin caught with circle hooks in the present study were hooked in the mouth or jaw (n=23) rather than internally or by foul hooking on the body (n=5), as was also noted by Horodysky and Graves (2005) for white marlin caught in the directed recreational fishery. In the present study, low numbers of animals caught on either hook types prevented robust comparisons of postrelease survival rates by hook type. More balanced comparisons of postrelease survival among hook types were precluded by both a limited number of expensive PSATs and the imposition of a domestic management measure that prohibited the use of J-style hooks in the U.S. pelagic longline fishery as of 5 August 2004 (FR, 2004). Although beyond the scope of this study, any additional changes in the fishing practices of this fishery, such as the varying lengths of "soak time" between overnight sets (swordfish) and daylight sets (tunas), may also affect the rates of postrelease survival of white marlin.

Ultimately, hooking location may be a more important factor than hook type for predicting postrelease survival. Three of the four PSATs attached to internally hooked animals in this study did not transmit data, although Prince et al. (2002b) reported encapsulated hooks from istiophorid viscera, indicating that internal hooking events are not necessarily fatal. The large percentage of white marlin (35.7%) hooked through the upper lateral palate into the eye or eye socket raises some concern. Istiophorid billfishes are considered to be primarily visual predators (Rivas, 1975) and damage to an eye would be expected to negatively affect the foraging ability of the animal. Billfish are known to have specialized muscle tissue that allows individuals to maintain elevated brain and eye temperatures (Block, 1986), and recent work has revealed color vision in some istiophorids (Fritsches et al., 2003). Dissections of sailfish have revealed that hookings in the eye socket often cause damage to the optic nerve and surrounding ocular musculature (Jolley[4]). The one fish caught with a circle hook through the eye socket in Horodysky and Graves (2005) survived for the entire 10-day deployment period, and in the present study, the seven animals hooked through the eye socket also all survived for their entire deployment periods, as did one white marlin caught with a circle hook through the eyeball. A tagged striped marlin in Domeier et al. (2003) with a punctured eye also survived for ten days, suggesting that this condition is not necessarily fatal over short durations, and healthy swordfish have been observed

[4] Jolley, J. W. 1977. The biology and fishery of Atlantic sailfish *Istiophorus platypterus*, from southeast Florida, 31 p. Fla. Mar. Res. Pub., contribution no. 298. Florida Dep. Natural Resources, Marine Research Laboratory, 100 Eighth Avenue SE, St. Petersburg, FL 33701.

with one healed ocular cavity (D. W. Kerstetter, personal observ.).

We observed a high percentage of hooked white marlin with associated eye damage, specifically in conjunction with circle hooks. In contrast, Horodysky and Graves (2005) noted only one animal out of 40 hooked through the eye with a circle hook. The difference between studies may be a factor of the hook sizes used in the fisheries; the recreational fishery generally uses much smaller circle hooks than the commercial pelagic longline fishery (7/0 and 9/0 sizes versus 16/0 and 18/0). Jolley[4] observed that for 134 (15.8%) of 848 sailfish caught recreationally with J-style hooks, the barbs exited near the eyes, noting that the distal lateral regions of the istiophorid mouth roof (those areas underlying the eyes) are thinly-covered muscle tissue rather than bone. A hook would therefore presumably pass much more easily through this tissue to the eye than if it encountered the lower jaw. Prince et al. (2002b) considered hooking through the upper palate potentially lethal, not only because of the opportunity for the hook to penetrate the occipital orbit, but also because of the tendency for J-style hooks in that location to compromise the integrity of the cranium, making it more susceptible to infection. Two tags that did not transmit data in our study were attached to fish caught with J-style hooks in the center of the upper palate. Borucinska et al. (2002) noted that for blue sharks (*Prionace glauca*) wounded by fishing hooks, an injury caused by a perforating hook may lead to systemic debilitation over longer time intervals than that typically measured with PSAT tags.

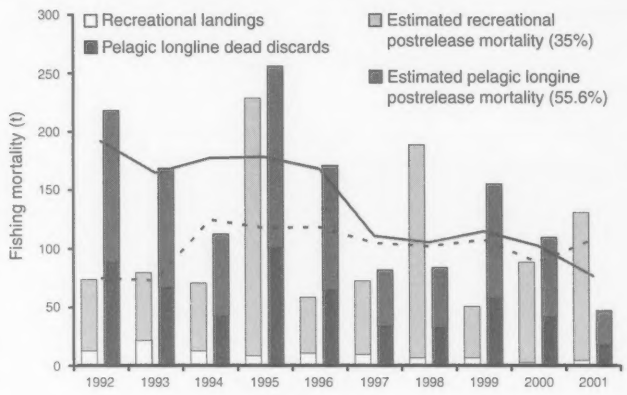

Figure 2

Calculated white marlin (*Tetrapturus albidus*) fishing mortality estimates in metric tons (t) for the recreational and pelagic longline fisheries of the United States. The bottom part of each bar represents the reported mortality in each fishery (recreational landings and commercial dead discards, respectively), while the top part of the bar represents the possible additional fishing mortality based on conservative assumptions of 35% postrelease mortality with J-style hooks for the recreational fishery (Horodysky and Graves, 2005) and 55.6% postrelease mortality with J-style hooks in the commercial pelagic longline fishery (present study). The solid line is the three-year running average for estimated total recreational mortality (reported and estimated postrelease mortality), and the dashed line is the estimated total commercial pelagic longline mortality.

The postrelease mortality rates obtained for white marlin from Horodysky and Graves (2005) and this study also allowed the estimation of total U.S. fishing mortality for this species. For the U.S. directed recreational fishery, the white marlin postrelease mortality rate (35% for J-style hooks; Horodysky and Graves, 2005) was applied to estimated yearly catch data and added to "best estimates" of the U.S. recreational landings (Goodyear and Prince, 2003). For the pelagic longline fishery, catch and condition at release data were obtained from the NMFS Pelagic Observer Program database (Lee[5]). The 55.6% postrelease mortality rate (J-style hooks, nontransmitting tags as mortalities; present study) was applied to the number of white marlin released alive to obtain an estimate of the number of fish that died following release. Average underestimates of the actual white marlin fishing mortality to recreational fishery reported landings or to commercial fishery dead discards during this ten-year period were 88.6% and 61.6%, respectively.

Our analysis indicates that the directed U.S. recreational fishery may generate higher levels of white marlin fishing mortality than the U.S pelagic longline fishery in some years simply due to greater numbers of animals caught (Fig. 2). Because we chose the postrelease mortality estimates based on the historic terminal gear choices of J-style hooks, these results do not account for the probable decrease in total white marlin postrelease mortality resulting from mandated (pelagic longline) and voluntary (recreational) changes in the U.S. fisheries from J-style hooks to circle hooks. However, even this estimated magnitude of actual mortality incurred as the result of the U.S. recreational or pelagic longline fisheries results in the international pelagic longline fishery remaining the largest source of total white marlin fishing mortality in the Atlantic (ICCAT, 2005).

The results of this study clearly demonstrate that white marlin are capable of surviving the trauma associated with capture by pelagic longline fishing gear. Short-term survival of released white marlin was relatively high whether one discounted nontransmitting tags (89.5% survival) or considered nontransmitting

[5] Lee, D. 2004. Personal commun. NOAA/NMFS Southeast Fisheries Science Center, 75 Virginia Beach Dr., Miami, FL 33149.

tags to represent mortalities (62.9% survival). These estimates are similar in magnitude to that found for the larger blue marlin released from pelagic longline gear (79% survival; Kerstetter et al., 2003). The documented survival of white marlin indicates that current domestic and international management measures requiring live release from commercial pelagic longline gear will reduce fishing mortality on this species.

Acknowledgments

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Application of two methods for determining diet of northern fur seals (*Callorhinus ursinus*)

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Abstract—Examination of hard parts recovered from scats (feces) is currently the most common method for determining the diet of pinnipeds. However, large or sharp prey remains may be spewed (regurgitated) biasing prey composition and size estimations in diet studies based on scats. Percent frequency of occurrence (FO%) and age or size of selected prey remains recovered from northern fur seal (*Callorhinus ursinus*) scat (n=3444) and spew samples (n=267) collected from rookeries on St. George Island and St. Paul Island, Alaska, between 1990 and 2000 were compared to determine if a bias in prey composition and age or size estimations existed between scats and spews.

Overall prey composition was similar between sample type and location, but the relative FO% of primary prey (≥5%) varied by sample type and location. Age or size estimates of walleye pollock (*Theragra chalcogramma*) and of two species of gonatid squids (*Gonatopsis borealis* and *Berryteuthis magister*) were significantly larger in spews than in scats. Observed differences in FO% and estimated age or size of prey species whose remains were found in scats and spews likely result from size-selective digestion of prey remains. Scats were biased toward smaller prey remains, whereas spews were biased toward larger prey remains and cephalopod beaks. The percent overlap between age classes of walleye pollock caught by the commercial trawl fishery and age classes of walleye pollock consumed by northern fur seals varied noticeably between sample types for both islands (scats: St. George=15. 5%; St. Paul=4.1%; spews: St. George=94.6%; St. Paul=89.6%). These results demonstrate that the inclusion of multiple sampling methods allows for a more accurate assessment of northern fur seal prey occurrence and prey age and size.

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Pinniped diet analysis involves the identification of prey remains recovered from a variety of sample types. Prey remains are obtained from stomach lavage and enema procedures from feces (scats) and regurgitations (spews), and from stomachs and gastrointestinal tracts. Historically, northern fur seal (*Callorhinus ursinus*) diet studies have relied upon analysis of stomach and intestinal contents collected from scientific takes or harvested animals (Wilke and Kenyon, 1957; Kajimura, 1984; Bigg and Fawcett, 1985; Sinclair et al., 1994) and, more recently, scat samples (Sinclair et al., 1996; Antonelis et al., 1997). Because a thorough analysis of gastrointestinal contents generally requires the sacrifice of an animal, intact gastrointestinal specimens are no longer typically used in diet analyses. Lavage and enema procedures are also not widely used to describe the diet of the population because sample sizes are often small and animals may require chemical immobilization, thereby increasing the risk of injury or fatality (Antonelis et al., 1987; Harvey and Antonelis, 1994).

Presently, scats are the most commonly used sample type in pinniped diet analyses because they are easy to collect, abundant, and noninvasive (Harvey, 1989; Hammond and Prime, 1990). However, many studies have demonstrated the potential biases associated with this sampling method (Jobling and Breiby, 1986; Pierce and Boyle, 1991; Bowen, 2000), including the accumulation of cephalopod beaks in the stomach (Bigg and Fawcett, 1985; Gales et al., 1993; Harvey and Antonelis, 1994) and underestimation of size and frequency of occurrence of some prey species (Bigg and Fawcett, 1985; Harvey, 1989; Tollit et al., 1997). Captive feeding studies of numerous pinniped species have shown that factors such as species, sex, individual activity level, stomach size, gut length, prey digestibility, feeding regime, and meal size affect the degree of erosion and recovery of prey remains in scats (Harvey and Antonelis, 1994; Tollit et al., 1997; Marcus et al., 1998; Bowen, 2000; Orr and Harvey, 2001). Although studies have been conducted to account for these biases through the use of correction factors (Sinclair et al., 1994; Antonelis et al., 1997; Tollit et al., 1997), the different retention and digestive rates of prey remains in the stomach continue to be a leading criticism for diet studies in which scat samples alone are used.

Spews have been analyzed for several species of pinnipeds (Gales et al., 1993; Harvey and Antonelis, 1994; Kiyota et al., 1999; Lowry and Carretta, 1999; Kirkman et al., 2000). Spews contain prey remains such as fish bones, otoliths, and cephalopod beaks. Often these prey remains are too large to pass through the pyloric sphincter and are, therefore, regurgitated from the stomach (Bigg and Fawcett, 1985; Jobling and Breiby, 1986). Although spewings may be found in areas where pinnipeds come ashore, they are often less abundant

than scats (Jobling and Breiby, 1986; Gales et al., 1993) and have largely been excluded from pinniped diet analyses. Spews from northern fur seals are present on summer breeding islands, but diet studies that are based on spews are limited (Kiyota et al., 1999).

Our study is a comparative evaluation of diet based on scat and spew samples collected from northern fur seal breeding rookeries on two islands in the eastern Bering Sea. Prey remains in scat and spew samples were compared for prey species composition, and the age or size of walleye pollock (*Theragra chalcogramma*) and of two species of gonatid squids (*Gonatopsis borealis* and *Berryteuthis magister)* were estimated. Finally, we compared age classes of walleye pollock found in scats and spewings to age classes of walleye pollock caught by the commercial trawl fishery in management regions adjacent to the Pribilof Islands.

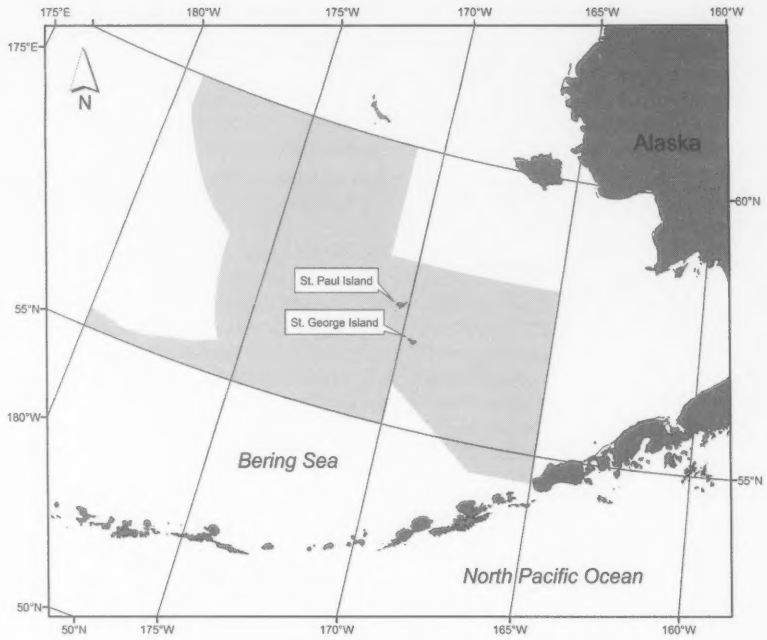

Figure 1

Location of St. George Island and St. Paul Island, within the Pribilof Islands, Alaska. Shaded area indicates walleye pollock (*Theragra chalcogramma*) commercial trawl fishery management areas surrounding the Phibilof Islands.

Materials and methods

Sample collection and processing

Scats and spews were collected opportunistically from rookeries on the Pribilof Islands (St. George and St. Paul), Alaska (Fig. 1), during the breeding season between 1990 and 2000. Samples collected from rookeries during this time (late July through September) were considered to be primarily from females of breeding age (Antonelis et al., 1997). Each scat and spew sample was placed in a plastic bag and frozen until it was analyzed in the laboratory. Samples were thawed and soaked in a mild emulsifying soap solution then rinsed through nested sieves of 4.75, 1.4, 1.0, and 0.5-mm mesh. Bones, otoliths, beaks, and eye lenses were recovered from the sieved samples and stored for analysis. Bones, otoliths, and eye lenses were stored dry in vials and beaks were stored in vials containing 50% isopropyl alcohol (Antonelis et al., 1997). Recovered diagnostic fish bones, otoliths, and cephalopod beaks were identified to the lowest possible taxon by comparing them to a reference collection. Distinctions, based on the morphological features of beaks, between some cephalopod species within the family Gonatidae were not possible. Therefore, identifications of four squid species known to occur in northern fur seal diet were categorized into two groups following Sinclair et al. (1994) and Antonelis et al. (1997) and are referred to as Gb-Bm (*Gonatopsis borealis and Berryteuthis magister*) and Gm-Gm (*G. madokai* and *G. middendorfii*). Additionally, distinctions between four gonatid species (*Eogonatus tinro*, *G. berryi*, *G. pyros*, and *G. onyx*), were difficult to determine from the morphological features of beak and, collectively, are referred to as "gonatid group I" in the present study.

Prey indices

Individual prey species and prey groups were analyzed according to their frequency of occurrence (FO) in scats and spews for both islands. The percent frequency of occurrence (FO%) was calculated by dividing the number of scats or spews containing a specific prey species or group by the total number of scats or spews containing identifiable prey remains. Data from each year were pooled for FO% calculations because of low sample sizes in some years. Prey species or groups with a FO% ≥5% when rounded to the nearest integer, for either island or sample type, were considered to be primary prey.

The minimum number of individuals (MNI) of each prey type was calculated for each sample, and summed over all samples. The cephalopod MNI was estimated by using the maximum count of either upper or lower beaks in each sample. Fish MNI was estimated by using the maximum count in each sample from left or right otoliths, plus half of the otoliths for which a side (right or left) could not be determined (Antonelis et al., 1997). Percent MNI (MNI%) was then calculated by

dividing the MNI of each prey species or group (for all samples) by the total MNI of all prey for samples that contained identifiable fish otoliths or cephalopod beaks (or both).

To determine if the occurrence of prey varied by island or sample type (or both), the presence or absence of the primary prey (n=number of scats with prey remains) was modeled as a binomial random variable by using generalized linear models with island, sample type, and the interaction of island and sample type as explanatory variables (S-PLUS 2000, Insightful Corp., Seattle, WA). The interaction was considered significant if adding the interaction significantly reduced the deviance in the model. If the interaction was significant, islands within each sample type or sample types within each island were compared, depending on whether sample type or island reduced more of the overall deviance. If the interaction was not significant, it was removed from the model, and island and sample type effects were tested. Even though data were insufficient to test for differences in prey occurrence between years, year was included in the model as an additive variable.

Comparisons of prey age and size

Recovered walleye pollock otoliths were assigned a condition grade ("good," "fair," or "poor") based on distinctive features such as sulcus definition, shape, chipping, breaks, and wear (Sinclair, 1988). Pollock otoliths of "good" or "fair" condition were measured lengthwise parallel to the sulcus to the nearest 0.1 mm using handheld digital calipers. A correction factor was applied to "fair" otoliths to account for loss of otolith length as a result of digestion (Sinclair, 1988; Antonelis et al., 1997). Fork lengths of prey were estimated by using regression formulae of otolith length against body length (Frost and Lowry, 1981) and age class was estimated from fork-length–age relationships (Sinclair et al., 1994). Pollock otoliths of "poor" condition were enumerated, but not measured, and were not included in prey size comparisons because of their high degree of erosion.

Pollock otoliths recovered from scat samples processed in the early 1990s were measured, but only age class estimations were recorded in the database. Therefore, to test how the size of walleye pollock otoliths varied by sample type and island, otoliths of "good" and "fair" grades were combined into two age categories; juvenile (0–2 age) and adult (3–5+ age) and each sample (scat or spew) was categorized as containing juvenile, adult, or mixed (juvenile and adult) pollock. Multidimensional contingency tables with island, sample type, and age category as variables were used to test interactive effects among variables. A saturated model including all variables and interactions was compared with restricted models by using chi-square goodness-of-fit test (S-PLUS 2000, Insightful Corp., Seattle, WA). Samples were pooled if sample type or island effects were conditionally independent, and two-dimensional contingency tables were then used to test variables that were not independent.

The size range of Gb-Bm consumed by northern fur seals was estimated by measuring the rostral length of lower beaks recovered from scat and spews. Rostral length was measured to the nearest 0.1 mm with an optical micrometer. Because cephalopod beaks are more resistant to digestion and to subsequent loss of length than are otoliths (Sinclair et al., 1996; Tollit et al., 1997), Gb-Bm lower beaks were not assigned condition grades prior to being measured. However, lower beaks showing excessive wear, such as a broken rostral tip, were not measured.

To evaluate Gb-Bm prey size differences between sample type and islands, we developed (using combined samples of both species) regression equations for lower beak rostral length (LRL) against dorsal mantle length (DML) and for DML against weight. Squid specimens were opportunistically collected from commercial pollock trawl fishery bycatch, research driftnets, and NOAA research vessel mid-water trawl operations between 1979 and 2000. Sampling areas were broad ranging throughout the North Pacific, at numerous localities in the eastern Bering Sea, Gulf of Alaska, and subarctic Pacific Ocean south of the western Aleutian Islands (Walker[1]).

The regression of LRL against DML for Gb-Bm was developed by using 757 lower beaks (n=482 Gb, 275 Bm) with a dorsal mantle length range of 21–386 mm and the DML-weight regression was developed by using 1676 lower beaks (n=1048 Gb, 628 Bm) with a dorsal mantle length range of 17–386 mm. The regression included size ranges of Gb-Bm found in northern fur seal scats and spews examined in the present study. Linear models were used to develop regressions of LRL (mm) against DML (mm) and DML against weight (grams):

$$DML = 39.37(LRL) - 0.50.$$

$$\mathrm{Log}(weight) = 2.87\big(\mathrm{Log}(DML)\big) - 4.16.$$

A high degree of correlation (LRL to DML $P<0.001$; $r^2=0.98$; SE=0.51); DML to weight $P<0.001$; $r^2=0.99$; SE=0.01) was found for both regression equations (Walker[1]). Gb-Bm DML data were log transformed and differences in DML between sample types and island were determined by comparing means with a two-sample t-test. Although the DML-weight regression is not used in the analysis, it is included here for future use by other researchers conducting bioenergetics studies.

Prey age or size estimations were limited to walleye pollock and Gb-Bm because sufficient numbers of otoliths or beaks of other primary fish and cephalopod prey species were not recovered from scat and spew samples, or because regressions for the species were unavailable.

[1] Walker, W. A. 2004. NMFS database. Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

Overlap between age classes of pollock consumed by northern fur seals and pollock caught by the commercial trawl fishery

Age-class distributions of walleye pollock in scat and spew samples were compared with pollock size-composition data in commercial midwater trawls (National Marine Fisheries Service, North Pacific Groundfish Observer Program). Trawl data included samples collected from August through September 1990 to 2000 in fishery management areas surrounding the Pribilof Islands (Berger[2]; Fig. 1) that encompass northern fur seal foraging habitat (Robson et al., 2004). Walleye pollock fork length from trawls was converted to age class by following the method of Sinclair et al. (1994) for determination of overlap with the age class of pollock consumed by northern fur seals (as estimated from scat and spew samples).

Results

Prey abundance

A total of 1127 scats and 204 spews from St. George Island and 2317 scats and 63 spews from St. Paul Island contained prey remains (Table 1). Prey species composition was similar between scats and spews for each island, but the relative importance of primary prey species based on FO% and MNI% varied by sample type and island (Table 2). Primary prey species (FO% ≥5%) found in both scats and spews consisted of gonatid group I, Gb-Bm, Gm-Gm, northern smoothtongue (*Leuroglossus schmidti*), Pacific herring (*Clupea pallasi*), Pacific salmon (*Oncorhynchus* spp.), Pacific sand lance (*Ammodytes hexapterus*), and walleye pollock (Fig. 2).

Significant interactions between sample type and island were found for Gb-Bm, Gm-Gm, Pacific salmon, and walleye pollock (Table 3); therefore the FO% of these prey was compared within island or sample type. The occurrence of Gb-Bm in scats versus spews from St. George Island was significantly different—spews having a higher FO% than scat. The FO% of Gb-Bm in scats versus spews collected from St. Paul Island was not significantly different. The FO% of walleye pollock was higher for St. George Island scats than for St. George Island spews. Pollock had the highest FO% of all prey in St. Paul Island scat and spews but was not significantly different between sample types. The FO% of Pacific salmon was significantly higher in spews than scat samples for both islands. The FO% of Gm-Gm was significantly higher in St. George Island spews than in St. Paul Island spews. Of the prey for which no interaction between sample type and island was observed, differences in the FO% of gonatid group I, northern smoothtongue, and Pacific sand lance were significant between islands and between sample types (Table 3). Pacific herring was only different between islands. Year of collection had a significant effect on the occurrence of all primary prey species except gonatid group I and was included in the model as an additive variable. Although scat and spew samples were collected during the same season each year, annual comparisons between sample types were not possible because of low sample size within years (Table 1).

Table 1

Numbers of northern fur seal (*Callorhinus ursinus*) scat and spew samples collected on St. George Island and St. Paul Island, Pribilof Islands, Alaska rookeries during the breeding season (late July–September), 1990–2000.

	St. George Island		St. Paul Island	
Year	Scats	Spews	Scats	Spews
1990	162	28	484	1
1991			109	5
1992	84	32	291	13
1993	10	1		
1994	184	46	230	3
1995	149	7	319	17
1996	141	11	337	14
1997	120	35	80	1
1998	199	24	207	5
1999			30	4
2000	78	20	230	
Total (*n*)	1127	204	2317	63

Variations in MNI% were observed between sample types and island for Gb-Bm and walleye pollock (Table 2). The MNI% of Gb-Bm was higher in spews than in scat samples for both islands. Conversely, the MNI% of walleye pollock was higher in scats than in spews for both islands. Scat and spew samples from St. George Island had higher MNI% of Gb-Bm than those collected from St. Paul Island. The MNI% of walleye pollock in both sample types from St. Paul Island was greater than the MNI% of walleye pollock from St. George Island in scats and spews.

Comparisons of prey age and size

A total of 1755 walleye pollock otoliths were recovered from 173 St. George Island scat samples containing walleye pollock and, of these, 1484 were determined to be in "good" or "fair" condition. Of the 152 walleye pollock otoliths recovered from 27 St. George Island spew samples, 105 were graded as "good" or "fair." From St. Paul Island, 17,827 of 20,062 walleye pollock otoliths recovered from 902 scat samples and 154 of 202 walleye pollock otoliths recovered from 23 spew samples were determined to be

[2] Berger, J. 2004. NMFS. database. Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

Table 2

Percent frequency of occurrence (FO%) and percent minimum number of individuals (MNI%) of prey species recovered in northern fur seal (*Callorhinus ursinus*) scat and spew samples collected on St. George Island and St. Paul Island, Pribilof Islands, Alaska, during the breeding season (late July–September), 1990–2000. Table only includes prey species with an FO%≥1% within either sample type and on either island.

	St. George Island				St. Paul Island			
	FO%		MNI%		FO%		MNI%	
Prey species	Scats	Spews	Scats	Spews	Scats	Spews	Scats	Spews
Atka mackerel (*Pleurogrammus monopterygius*)	2.1	1.0	<1.0		3.6		<1.0	
Bathylagidae sp.	1.8		<1.0		<1.0		<1.0	
Gb-Bm (*Gonatopsis borealis* and *Berryteuthis magister*)	22.7	55.4	62.5	94.6	5.6	9.5	5.3	32.7
Gm-Gm (*Gonatus madokai* and *Gonatus middendorfii*)	7.4	14.7	2.8	<1.0	9.8	3.2	3.5	1.6
Gonatid group I (*E. tinro*, *G. berryi*, *G. onyx*, and *G. pyros*)	3.9	23.5	1.4	2.1	1.1	4.8	<1.0	2.0
Gonatidae sp.	1.4	1.0	<1.0	<1.0	<1.0		<1.0	
Gonatus sp.	<1.0	2.9	<1.0	<1.0	<1.0		<1.0	
Greenling sp. (*Hexagrammos* sp.)	<1.0				1		<1.0	
Northern lampfish (*Stenobrachius nannochir*)	1.0	<1.0	<1.0		<1.0		<1.0	
Northern smoothtongue (*Leuroglossus schmidti*)	7.4		5.4		1.7		1.5	
Pacific cod (*Gadus macrocephalus*)	<1		<1.0		1		<1.0	
Pacific herring (*Clupea harengus*)	2.0	2.0	<1.0		3.9	4.8	<1.0	
Pacific salmon (*Onchorhynchus* spp.)	14.8	29.4	<1.0		7.5	34.9	<1.0	
Pacific sand lance (*Ammodytes hexapterus*)	2.6		<1.0		8.9		1.1	
Pacific sandfish (*Trichodon trichodon*)	<1.0		<1.0		2	1.6	1.3	
Sablefish (*Anoplopoma fimbria*)	<1.0				1.3			
Unidentifed cephalopod	2.3	4.9	<1.0		1.2		<1.0	
Unidentified fish	27.6	3.9	<1.0		31.2		<1.0	
Unidentified gadid	17.3	15.2	<1.0		33.4	6.3	2.1	
Walleye pollock (*Theragra chalcogramma*)	59.6	36.8	22.9	2.1	71	69.8	82.3	63.3
Sample size (*n*)	(1127)	(204)	(5043)	(5754)	(2317)	(63)	(19,028)	(251)

in "good" or "fair" condition. The occurrence of walleye pollock age classes determined from otolith measurements varied by sample type (Fig. 3).

A multidimensional contingency analysis showed that sample type was independent of island (P=0.087, χ^2=6.26, df=3); therefore data from St. George and St. Paul Islands were pooled to test for differences in age class of prey between sample types. Spews contained a larger percentage of adult pollock (88.0%, P<0.001, χ^2=260.27, df=1) and a smaller percentage of juvenile pollock (9.1%, P<0.001, χ^2=180.91, df=1) than scats. There was not a significant difference in the occurrence of mixed-age pollock between scats (6.4%) and spews (4.0%) (P=0.490, χ^2=0.47, df=1) and only 71 of 1125 (6.3%) samples contained both age classes. A total of 2856 and 5030 Gb-Bm lower beaks were recovered and measured from 225 scat samples and 111 spew samples, respectively, collected at St. George Island (Fig 4.). A total of 719 Gb-Bm lower beaks were recovered and measured from 110 St. Paul Island scat samples and 47 Gb-Bm lower beaks were recovered and measured from five St. Paul Island spew samples. The mean DML of Gb-Bm in St. George Island scat and spew samples was 69 mm (SE=0.10) and 82 mm (SE=0.14), respectively. The mean DML of Gb-Bm in St. Paul Island scat samples was 67 mm (SE=0.21) and in spew samples was 101 mm (SE=6.35). Gb-Bm data were log transformed to meet assumptions of normality for island and sample-type size comparisons. The DML of Gb-Bm estimated from beaks recovered from spew samples was significantly larger than the DML estimated from beaks recovered from scat samples collected from both islands (two-sample t-test, P<0.001 for St. George Island and St. Paul Islands). The DML of Gb-Bm from St. George Island scats was significantly larger than that form St. Paul Island scats (two-sample t-test, P<0.001). In spew samples, estimated Gb-Bm DML was significantly larger on St. Paul Island than on St. George Island (two-sample t-test, P<0.001). However, the number of spews collected from the two islands were highly unequal (n=204, St. George Island; n=63, St. Paul Island).

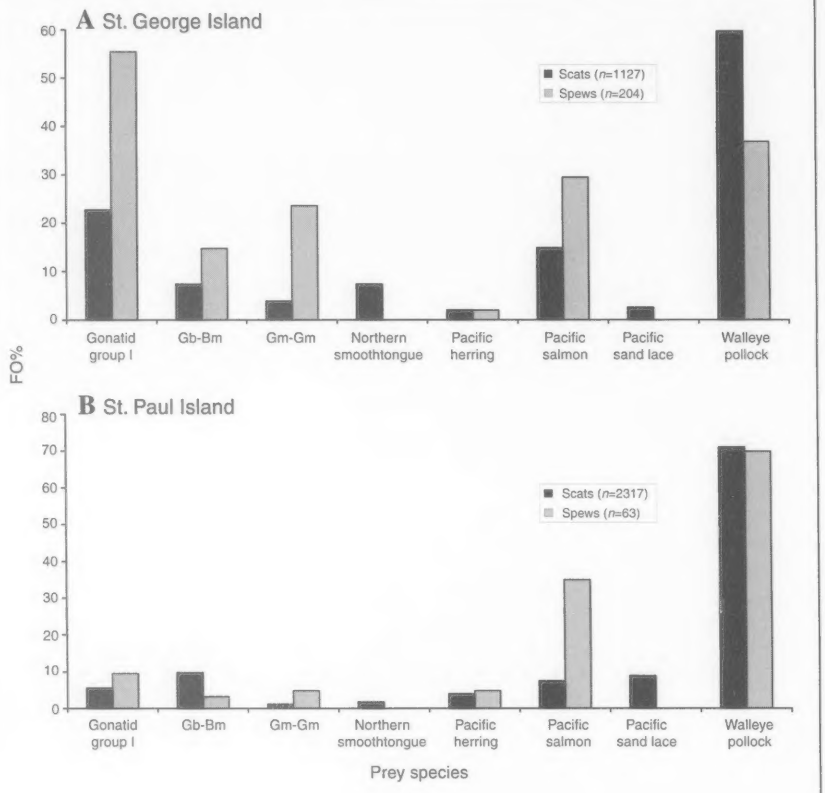

Figure 2

Percent frequency of occurrence (FO%) of primary prey species (FO%≥5%) recovered from northern fur seal (*Callorhinus ursinus*) scats and spews collected from rookeries on (**A**) St. George Island and (**B**) St. Paul Island, Pribilof Islands, Alaska during the breeding season (late July–September), 1990–2000. Gonatid group I includes *E. tinro*, *G. berryi*, *G. onyx*, and *G. pyros*.

Overlap between age classes of pollock consumed by northern fur seals and pollock caught by the commercial trawl fishery

The percent overlap between age classes of walleye pollock caught by the commercial trawl fishery and those consumed by northern fur seals varied between sample types for both islands. Minimal overlap was observed between age classes of pollock found in St. George Island and St. Paul Island scats and those taken by the commercial trawl fishery (St. George Island=15.5%; St. Paul Island=4.1%, Fig. 3). However, the percentage of overlap between age classes of pollock found in St. George Island and St. Paul Island spews and the age classes of pollock taken in commercial trawls was considerable (St. George Island=94.6%; St. Paul Island=89.6%, Fig. 3).

Discussion

Northern fur seal diet studies conducted since the 1980s have primarily used scat samples to determine prey species and size. Despite the presence of spews on rookery and haul-out beaches, only Kiyota et al. (1999) has utilized spews to study northern fur seal diet. Kiyota et al. (1999) examined spews and scats collected from haul-outs (subadult male dominated) and found differences in the prey remains recovered between sample types. We compared the diet of adult female northern fur seals using scats and spews collected from rookeries on the Pribilof Islands over an eleven-year period. We observed differences in the percent frequency of occurrence (Fig. 2) and the estimated age or size (Figs. 3 and 4) of prey between scats and spews. Additionally, the degree of overlap between age classes of walleye pollock consumed by northern fur seals and those caught in

commercial fishery trawls varied considerably by sample type (Fig. 3). These findings highlight the potential limitations of a single sample type, such as scats, and demonstrate that a combination of scat and spew samples can provide a more complete description of northern fur seal diet.

The differences in prey occurrence that were observed among northern fur seal scats and spews in our study may have resulted from the accumulation of irregularly shaped or large prey parts in the stomach (Kiyota et al., 1999). Large cephalopod beaks and fish bones accumulate near the pyloric sphincter and are regurgitated from the stomach, whereas small prey parts pass through the digestive system and are recovered in scats (Bigg and Fawcett, 1985). The different rates of retention of prey parts in northern fur seal stomachs would, therefore, bias scat samples toward small prey species or small bones of large prey species and spew samples toward large prey and cephalopods. For example, the FO% of Pacific salmon, a large boned fish species, was higher in spews than in scats. Kiyota et al. (1999) also observed a higher occurrence of Pacific salmon in spews than in scats of juvenile male northern fur seals from St. Paul Island. The FO% we observed for northern smoothtongue and Pacific sand lance also support a prey species bias between sample types; the small forage fish were among primary prey species found in scat samples but were absent from spew samples.

In addition to differences observed between sample types, we found that the occurrence of primary prey species varied between islands. Specifically, the FO% of gonatid group I, Gb-Bm, Gm-Gm, and walleye pollock varied considerably between sample types and islands, and significant interactions between sample type and island were observed for a number of these species. Walleye pollock was the highest occurring prey in St. George Island scats, but the FO% was significantly lower in spew samples. On St. Paul Island, walleye pollock was the dominant prey species, but the FO% did not differ between scats and spews. Similarly, the FO% of Gb-Bm at St. Paul Island did not differ between sample types. However, the FO% of Gb-Bm was significantly higher in spews than in scats on St. George Island. The FO% of gonatid group I differed both between sample types and between islands; the occurrence of this group was highest in spews, and in samples from St. George Island. Overall, cephalopods occurred at higher frequencies on St. George Island than on St. Paul Island for both sample types. The lone exception was Gm-Gm, which had a lower frequency on St. George Island for scats. Observed differences in cephalopod and walleye pollock occurrence between St. George

Table 3

Results of generalized linear model comparing occurrence of primary prey species identified in northern fur seal (*Callorhinus ursinus*) scat and spew samples collected on St. George Island and St. Paul Island, Pribilof Islands, Alaska, during the breeding season (late July–September), 1990–2000. The following abbreviations are used for cephalopod prey: Gb-Bm (*Gonatopsis borealis* and *Berryteuthis magister*), Gm-Gm (*Gonatus madokai* and *Gonatus middendorfii*), and gonatid group I (*Eogonatus tinro, Gonatus berryi, G. onyx*, and *G. pyros*).

	Year			Interaction (island × sample type)			Islands (St. Paul and St. George)			Sample type (scat and spew)			
Prey	χ^2	df	P	χ^2	df	P	χ^2	df	P	χ^2	df	P	
Gb-Bm	47.18	10	<0.0001	4.12	1	0.0424		—		1.95	1	0.1625	St. Paul only
		—			—			—		91.42	1	<0.0001	St. George only
Gm-Gm	118.14	10	<0.0001	8.37	1	0.0038	0.78	1	0.3771 scats only		—		
		—			—		3.84	1	0.0500 spews only		—		
Gonatid group I	17.31	10	0.0678	0.74	1	0.3908	40.12	1	<0.0001	78.10	1	<0.0001	
Northern smoothtongue	70.25	10	<0.0001	0.00	1	0.9862	44.18	1	<0.0001	25.29	1	<0.0001	
Pacific herring	90.37	10	<0.0001	0.03	1	0.8709	6.26	1	0.0124	0.10	1	0.7559	
Pacific salmon	97.94	10	<0.0001	9.70	1	0.0018		—		37.81	1	<0.0001	St. Paul only
		—			—			—		19.59	1	<0.0001	St. George only
Pacific sand lance	57.77	10	<0.0001	0.00	1	0.9887	56.98	1	<0.0001	19.00	1	<0.0001	
Walleye pollock	199.41	10	<0.0001	11.94	1	0.0005		—		0.29	1	0.5921	St. Paul only
		—			—			—		41.46	1	<0.0001	St. George only

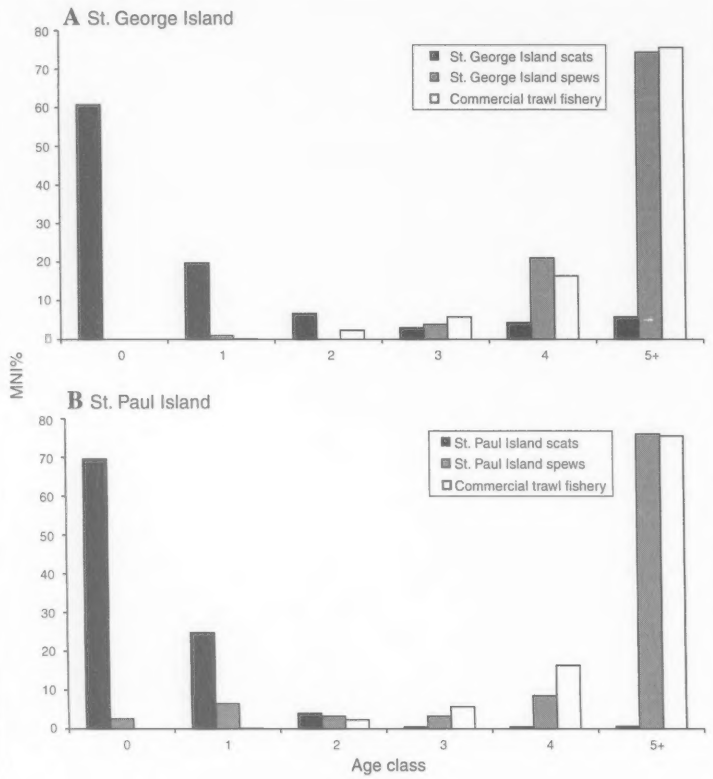

Figure 3

Percent minimum number of individuals (MNI%) of walleye pollock (*Theragra chalcogramma*) age classes recovered from northern fur seal (*Callorhinus ursinus*) scats and spews containing measurable pollock otoliths collected from rookeries on (**A**) St. George Island (1484 otoliths from 173 scat samples; 105 otoliths from 27 spew samples) and (**B**) St. Paul Island (17,827 otoliths from 902 scat samples; 154 otoliths from 23 spew samples), Pribilof Islands, Alaska, during the breeding season (late July–September), 1990–2000. Also shown is the MNI% of walleye pollock age classes caught by the commercial trawl fishery between August and September 1990–2000 in fishery management areas surrounding the Pribilof Islands, Alaska.

Island and St. Paul Island samples are likely related to the availability of prey within reach of female fur seals, which varies according to the physical and biological environment surrounding each island (Sinclair et al., 1994; Antonelis et al., 1997; Robson et al., 2004).

The occurrence of important prey species in scat samples was consistent with previous analyses of northern fur seal scat and stomach samples. However, there were considerable differences in prey occurrence between spews samples and previous studies (Kajimura, 1984; Sinclair et al., 1994, 1996; Antonelis et al., 1997). In northern fur seal diet studies based on analysis of the entire gastrointestinal tract adult females were found to primarily consume juvenile walleye pollock and gonatid squid (Sinclair et al., 1994; 1996). Likewise, diet studies based on scat samples had the highest occurrences of walleye pollock and gonatid squid (Antonelis et al., 1997). Although we observed a similar FO% of walleye pollock in our scat samples, the FO% of gonatid squid and Pacific salmon were significantly higher among spews compared to previous studies based on scat and G.I. tract samples. Thus, it is likely that the importance of some prey species, such as gonatid squids and Pacific salmon, has been underestimated in previous diet studies (e.g., Antonelis et al., 1997).

Significant differences in the size of Gb-Bm were observed between scat and spew samples, demonstrating size-related digestive biases between sample types.

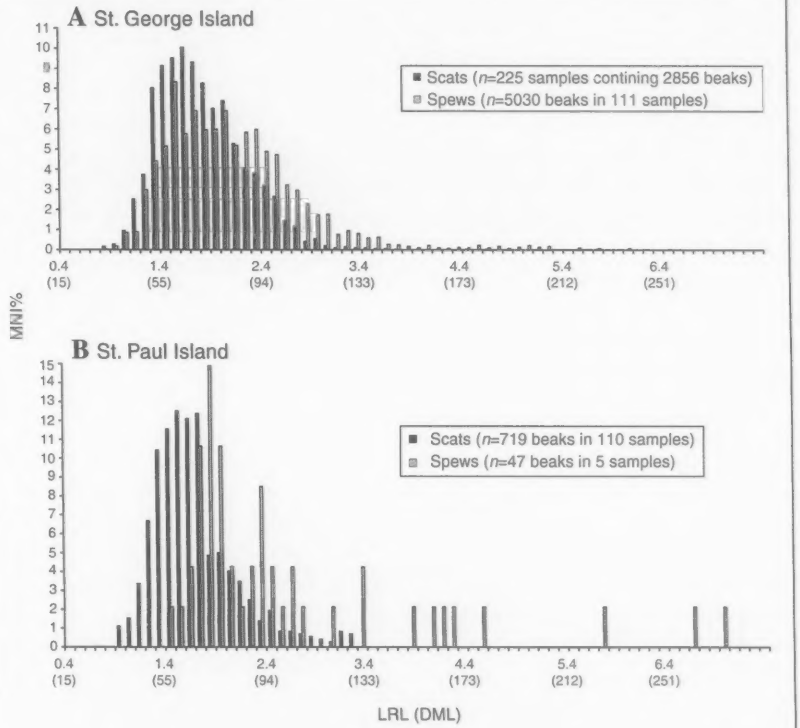

Figure 4

Percent minimum number of individuals (MNI%) of *Gonatopsis borealis* and *Berryteuthis magister* (Gb-Bm) lower rostral length (LRL) and dorsal mantle length (DML) in mm recovered from northern fur seal (*Callorhinus ursinus*) scats and spews containing measurable Gb-Bm beaks collected from rookeries on (**A**) St. George Island and (**B**) St. Paul Island, Pribilof Islands, Alaska, during the breeding season (late July–September), 1990–2000.

The dorsal mantle length size of Gb-Bm estimated from lower beaks was significantly larger in spew samples than scat samples (Fig. 4). Digestive biases relating to cephalopod beak size have also been observed in northern fur seal G.I. tracts (Yonezaki et al., 2003), as well as in Australian fur seal (*Arctocephalus pusillus doriferus*; Gales et al., 1993) and California sea lion (*Zalophus californianus*; Lowry and Carretta, 1999) spews and scats. Owing to limited taxonomic resolution of squid species in previous northern fur seal diet studies, direct comparisons of Gb-Bm size were not possible. For instance, Sinclair et al. (1994) presented DML size ranges of beaks recovered from stomachs, but, the cephalopod groups Gb-Bm and Gm-Gm were combined for analysis and were reported as gonatid squid.

We observed a greater percentage of adult walleye pollock in spew than in scat samples (Fig. 3). In addition, few scat and spewing samples were found to contain otoliths from both juvenile and adult age categories, further demonstrating size-related digestive biases of prey remains between sample types. The differences in walleye pollock age classes between scat and spew samples seem to indicate that size estimations of pollock consumed by northern fur seals have likely been underestimated in previous studies using G.I. tracts and scats (Sinclair et al., 1994, 1996). Northern fur seal diet studies based on analysis of the entire G.I. tract have shown that adult females consume primarily juvenile walleye pollock (Sinclair et al., 1994, 1996). However, biases associated with the retention of large prey remains are inherent in studies based on G.I. tract samples (Pierce and Boyle, 1991; Gales et al., 1993), and size-selective relationships between prey otolith size and sample type have been documented for northern fur seals (Kiyota et al., 1999; Yonezaki et al., 2003).

Data that accurately describe the ages of walleye pollock consumed by northern fur seals are critical for assessing potential competition with the commercial trawl fishery, which focuses on adult pollock. Previous northern fur seal diet analyses using scat and G.I tract

samples have revealed that northern fur seals primarily consume juvenile walleye pollock (Sinclair et al., 1994, 1996), indicating that there is limited competition between northern fur seals and the commercial trawl fishery. When walleye pollock age class was estimated from scats collected from 1990 to 2000, we found minimal overlap between the age classes of pollock consumed by northern fur seals and age classes of pollock caught by the commercial fishery during this time (Fig. 3). However, when spew samples were used to estimate age/size of fur seal prey, a high degree of overlap between age classes of pollock consumed by northern fur seals and pollock caught by the commercial fishery was observed (Fig. 3).

Because of the protective measures that resulted in closures of fisheries in Steller sea lion (*Eumetopias jubatus*) critical habitat, there is concern that fishery pressures in waters surrounding the Pribilof Islands may increase (NMFS[3]). Approximately 75% of the global northern fur seal breeding population inhabits the Pribilof Islands during the summer months (Loughlin et al., 1994) and recent estimates indicate a population decline. The total number of adult males on St. George and St. Paul Islands decreased by 13.4% and 2.8%, respectively, from 2002 to 2003 (Towell et al., 2006; York et al., 2005). Pup production also declined by >5% per year between 1998 and 2002 on both islands (York et al., 2005). At present, the cause of decline is uncertain but there is concern that increased fishing activity in waters surrounding the Pribilof Islands may adversely affect the northern fur seal population. We found that the occurrence and the age or size of some important prey species (such as walleye pollock) has been underestimated in previous northern fur seal diet studies in which only scat samples were used. Because some of these species are also commercially important, northern fur seal conservation and fishery management decisions should incorporate diet-related information acquired from multiple noninvasive sampling methods. This approach would allow better interpretation of northern fur seal dietary requirements, thereby providing a more accurate estimation of the extent to which protective measures in and around the Pribilof Islands should be instituted.

Scat and spew samples were collected simultaneously from the same rookeries on the Pribilof Islands during the breeding season; therefore we do not believe our results were affected by sampling effort. The discrepancies in sample sizes observed in this study may be the result of northern fur seal foraging behavior. Satellite tracking and behavioral studies of female northern fur seals have indicated that individual at-sea foraging trips may range between 6 and 10 days on average (Loughlin et al., 1987; Gentry, 1998; Robson et al., 2004). The accumulation of large cephalopod beaks and fish bones near the pyloric sphincter during this time may have irritated the stomach, causing the fur seals to regurgitate prey remains while at sea prior to their return to the rookeries. Although we do not know the regurgitation rates of fur seals, a tendency to regurgitate food during active digestion would explain the differences in sample size between spew and scat samples found on rookeries of the Pribilof Islands. Differences in proportions of sample types also have been observed on northern fur seal haul-outs (Kiyota et al., 1999), as well as on California sea lion haul-outs (Lowry and Carretta, 1999) and on Australian fur seal rookeries and haul-outs (Gales et al., 1993). Despite the skewed sample sizes between scats and spews in the present study, the observed differences in FO% and estimated age or size of prey between sample types were similar for both islands and were consistent with previous pinniped diet studies comparing scat and spew samples (e.g., Gales et al., 1993, Kiyota et al., 1999).

The various sampling methods used in pinniped diet analyses each have associated biases and sources of error that must be considered. The reliance upon any one sample type in diet assessments will limit one's ability to completely describe prey composition and prey size. Although our results corroborate the findings of previous diet studies with regard to the primary prey consumed by northern fur seals, this study demonstrates that using multiple sampling methods allows for a more accurate assessment of occurrence and age or size of prey.

[3] NMFS (National Marine Fisheries Service). 2001. Steller sea lion protection measures: final supplemental environmental impact statement, 3 volumes. NMFS, NOAA, Alaska Region, P.O. Box 21668, Juneau, AK 99802-1668.

Acknowledgments

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Abstract—Estimates of the abundance of American horseshoe crabs (*Limulus polyphemus*) are important to determine egg production and to manage populations for the energetic needs of shorebirds that feed on horseshoe crab eggs. In 2003, over 17,500 horseshoe crabs were tagged and released throughout Delaware Bay, and recaptured crabs came from spawning surveys that were conducted during peak spawning. We used two release cohorts to test for a temporary effect of tagging on spawning behavior and we adjusted the number of releases according to relocation rates from a telemetry study. The abundance estimate was 20 million horseshoe crabs (90% confidence interval: 13–28 million), of which 6.25 million (90% CI: 4.0–8.8 million) were females. The combined harvest rate for Delaware, New Jersey, Virginia, and Maryland in 2003 was 4% (90% CI: 3–6%) of the abundance estimate. Over-wintering of adults in Delaware Bay could explain, in part, differences in estimates from ocean-trawl surveys. Based on fecundity of 88,000 eggs per female, egg production was 5.5×10^{11} (90% CI: 3.5×10^{11}, 7.7×10^{11}), but egg availability for shorebirds also depended on overlap between horseshoe crab and shorebird migrations, density-dependent bioturbation, and wave-mediated vertical transport.

Abundance of adult horseshoe crabs (*Limulus polylphemus*) in Delaware Bay estimated from a bay-wide mark-recapture study

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The American horseshoe crab (*Limulus polyphemus*), having persisted largely unaltered for millions of years, is now central to a modern management debate of conflicting interests by commercial watermen, birdwatchers, biopharmaceutical companies, and eco-tourists (Odell et al., 2005). The management controversy is most acute in the Delaware Bay region where the high abundance of horseshoe crabs has resulted in the dependence of migrant shorebirds on horseshoe crab eggs to fuel their northern migration to nesting grounds (Botton and Harrington, 2003).

Because management goals have linked the horseshoe crab fisheries to the viability of other species, such as migrant shorebirds (ASMFC[1]), it is not sufficient to manage on the basis of typical reference points, such as maximum sustainable yield, because sustainable harvest is not the primary issue. In Delaware Bay, the viability of shorebirds has taken precedence in decision making (Botton and Harrington, 2003; Baker et al., 2004). Effective management should reference a critical threshold of horseshoe crab abundance that provides sufficient eggs and should sustain that threshold. Thus, abundance becomes a critical parameter because abundance estimates are useful for predicting the egg biomass that is available to migrant shorebirds and for assessing harvest rate.

Horseshoe crabs bury their eggs in beach sediment, typically 15 to 20 cm deep (Shuster and Sekiguchi, 2003). Eggs are exhumed to the beach surface and become available to foraging shorebirds through a process of entrainment in activated sediment, followed by vertical transport into surface sediments. Nest disturbance, which precedes entrainment of eggs, is predominantly due to bioturbation; whereas wave energy is only a contributing factor because typical estuarine waves do reach nest depth (Jackson et al., 2005). Given a relationship between egg exhumation and spawning density, egg availability could be predicted from current and projected horseshoe crab abundance.

[1] ASMFC (Atlantic States Marine Fisheries Commission). 1998. Interstate fishery management plan for horseshoe crab. Fishery Management Report No. 32, 58 p. ASMFC, 1444 Eye Street, NW, Sixth Floor, Washington, DC 20005.

Thus, studies to estimate abundance are an important step in the process of managing horseshoe crabs to meet the energetic needs of shorebirds.

We used results from a bay-wide mark-recapture effort during spring 2003 to estimate horseshoe crab abundance. Underlying assumptions of mark-recapture methods were accounted for in our study design and were evaluated during analysis. Recapture effort was distributed over Delaware Bay beaches by involving participants of a bay-wide spawning survey. We related our abundance estimates to reported landings to assess the recent harvest rate and used published fecundity estimates to predict egg production.

Materials and methods

We captured, tagged, and released horseshoe crabs from boats during two periods in 2003: a prespawning-season period (abbreviated to "preseason" in this article) from 26 March to 8 May and a prepeak-spawning period (abbreviated to "prepeak") from 28 to 30 May 2003. The numbers of crabs tagged were 7221 and 10,322 during the preseason period and prepeak period, respectively. The target population was adult horseshoe crabs that were present in Delaware Bay to spawn. One boat fished throughout the bay during the preseason period, and three boats fished nearshore during the prepeak period (Fig. 1). Prepeak period captures took place within strata of equal length along the Delaware Bay shoreline (Fig. 1). During the prepeak period, two boats fished in New Jersey, but only one boat fished in Delaware because of a lack of funding. Because of the additional boat in New Jersey, fishing effort and the number of crabs tagged were higher in New Jersey. Any animal injured during capture was culled and not tagged. Adult males and females were tagged with standard button tags. Tags were 4.4 cm in diameter, bore a unique tag number and carried instructions on the tag for reporting a captured tag. Further detail on tags and tagging methods are described in Brousseau et al. (2004).

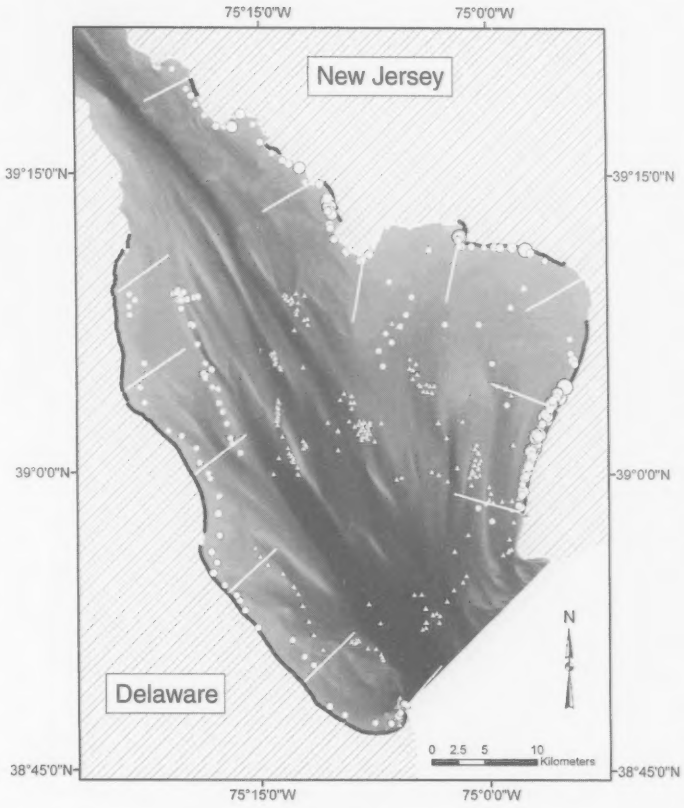

Figure 1

Locations in Delaware Bay where horseshoe crabs (*Limulus polyphemus*) were tagged and released. Size of symbols are graduated to reflect size of catches, and symbol style reflects whether releases occurred during the prespawning season period (26 March to 8 May 2003; triangle) or prepeak-spawning period (28–30 May 2003; circle). White lines perpendicular to the shoreline indicate strata within which catch effort during prepeak-spawning period was equally distributed. Black lines along the shore indicate approximate locations of spawning areas.

Recaptured tags came from the Delaware Bay spawning survey during the peak period of spawning (29 May, 31 May, and 2 June 2003). Although the spawning survey was conducted during spring tides in May and June, the recapture period for abundance estimation was limited to the peak spawning period to help satisfy the assumption of population-closure during the time of mark-recapture study (Borchers et al., 2002). Spawning survey volunteers were instructed to count all horseshoe crabs in sample quadrats and record tags that they encountered inside and outside of the sample quadrats. Flashlights were used when the survey occurred after dark. During the spring tide period around the new moon (29 May to 2 June 2003), 23 beaches were surveyed throughout Delaware Bay (Smith and Bennett[2];

[2] Smith, D. R., and S. Bennett. 2004. Horseshoe crab spawning activity in Delaware Bay: 5 years of a standardized and statistically-robust survey, 10 p. Report to the ASMFC Horseshoe Crab Management Board, Atlantic States Marine Fisheries Commission, Washington DC. Website: http://www.lsc.usgs.gov/aeb/2065/isa%20report%2005.pdf [accessed on 21 October 2005].

Fig. 1). The design of the spawning survey is described in Smith et al. (2002).

Mark-recapture methods

We took two approaches to estimate abundance. The first was an application of Chapman's modification of the Petersen estimator (Borchers et al., 2002). We applied the Petersen estimator separately for each of the two release periods and the three spawning survey dates. In addition, we combined the releases and recaptures for a pooled Petersen estimate.

The second approach was based on an extension of a likelihood presented by Borchers et al. (2002: p. 118, Eq. 6.11). We extended the likelihood to allow for a temporary effect on spawning behavior due to the capture and tagging process by including separate recapture probabilities for each release cohort. The extended likelihood was

$$L_s^* = \prod_{s=1}^{3} \binom{N - M_{\bullet s}}{u_s} p_s^{u_s} (1-p_s)^{N - M_{\bullet s} - u_s} \binom{M_{1s}}{m_{1s}} p_s^{m_{1s}} (1-p_s)^{M_{1s} - m_{1s}} \binom{M_{2s}}{m_{2s}} (p_s^*)^{m_{2s}} (1-p_s^*)^{M_{2s} - m_{2s}}$$

where N = the abundance at the start of the recapture period at the end of May 2003;
M_{1s} = the number of preseason tagged animals at large at time s;
M_{2s} = the number of prepeak tagged animals at large at time s ($M_{\bullet s} = M_{1s} + M_{2s}$);
m_{1s} and m_{2s} = the recaptures of preseason and prepeak tagged animals at time s;
u_s = the survey count of untagged at time s;
p_s = the capture probability for untagged and preseason tagged animals at time s; and
p_s^* = the capture probability of prepeak tagged animals at time s.

We also fitted a likelihood that set all recapture probabilities to be constant through time, i.e., $p_s = p$ for all recapture surveys, which reduces to Borchers' original likelihood (Borchers et al., 2002: p. 118, Eq. 6.11).

We used maximum likelihood methods to estimate abundance $\hat{N}$ and recapture probabilities ($\hat{p}_s, \hat{p}_s^*$). We used the Petersen estimate for the initial value for $\hat{N}$ and used m_s/M_s as the initial value for recapture probabilities. Profile-likelihood intervals were calculated for the abundance estimates (Borchers et al., 2002). MathCad (vers. 12, Mathsoft Engineering and Education Inc., Cambridge, MA) and SAS (vers. 9, SAS Institute Inc., Cary, NC) were used to find numerical solutions to the likelihood and profile-likelihood equations.

The following assumptions underlie the mark-recapture methods that we applied (Borchers et al., 2002):

1 No emigration or mortality occurred during the period between release and recapture;
2 the tagged animals represented an adequate sample;
3 animals were captured independently of one another;
4 tags were not lost or overlooked; and
5 recapture probability depended only on recapture occasion, was equal among animals of the same sex, and was equal for tagged and untagged animals.

The study was designed through the timing and distribution of releases and recaptures to meet the first two assumptions. The prepeak releases and recaptures were designed to be close in time to meet the assumptions of no emigration and no mortality. Immigration occurred during the time between preseason release and recapture; therefore we estimated the number of adults in Delaware Bay at the time of recapture, which was at the end of May in 2003 (Skalski and Robson, 1992). Some mortality occurred during the time between preseason release and recapture that we were not able to account for; however, we expect that mortality was similar for tagged and untagged animals. We ensured that both initial capture and recaptures were spatially distributed by distributing the releases throughout Delaware Bay during preseason tagging and within strata during prepeak tagging effort (Fig. 1) and by distributing recapture effort systematically by means of the spawning survey (Smith et al., 2002). The third assumption could be violated if horseshoe crabs moved locally in groups. However, recaptures came from widely spaced quadrats, so that even if the animals moved in groups, the whole group was unlikely to be recaptured within single quadrats. Although tag loss could be a significant factor over an extended period, we did not believe that significant tag loss occurred, especially over the five days from prepeak release to recapture period (28 May to 2 June 2003). In a tag-loss study conducted at the United States Geological Survey Leetown Science Center with identical tags, no tag loss over ≥60 days was reported, indicating that tag loss between preseason and recapture periods would not have been significant (Crawford[3]). Tags could have been overlooked during the spawning survey. Females bury themselves in beach sediment during spawning, and their tags could have been readily overlooked. In contrast, males do not bury themselves and the 4.4 cm white button tag is highly visible in daylight or when illuminated by flashlight. Nevertheless, tags on males could have been obscured when the horseshoe crabs piled up during peak spawning. Thus, we restricted our mark-recapture analysis to male horseshoe crabs that were counted and recaptured within 1-m^2 quadrats when surveyors were focusing on a small area.

[3] Crawford, E. 2003. Unpubl. data. USGS-Leetown Science Center, 11649 Leetown Road, Kearneysville, WV 25430

We limited mark-recapture estimates to males because capture probability was not equal for males and females as evidenced by recapture rates. Ratios of males and females captured for the tagging study were used to estimate total abundance with the equation

$$\hat{N} = \hat{N}_m / R_m,$$

where $\hat{N}_m$ = abundance of males; and
R_m = the ratio of males to the total captured.

Abundance of females was estimated by subtraction, i.e., by $\hat{N}_f = \hat{N} - \hat{N}_m$.

We used patterns of recaptures among preseason releases (released from 26 March to 8 May 2003) versus prepeak releases (released from 28 to 30 May 2003) to test the assumption that tagging did not affect spawning behavior. One approach was to use a contingency table analysis that included a comparison of risks of recapture between animals tagged during preseason and prepeak periods. Another approach was based on the extended likelihood presented above (L_s^*), which included a separate set of recapture probabilities for preseason and prepeak released animals. In this way, the model allowed for a temporary effect on capture probability due to tagging, such as a temporary delay in spawning. We used model comparison techniques (i.e., Akaike's information criteria and likelihood ratio tests) to compare recapture probabilities among preseason and prepeak released animals (Burnham and Anderson, 1998).

Results from a telemetry study conducted in 2004 provided information on spawning behavior of horseshoe crabs caught and released from boats. In 2004, we attached radio transmitters to 60 adult males throughout the Delaware Bay prior to the spawning season. When the animals came on the beach to spawn the signals from the transmitters were recognized by one or more of the 14 fixed station receivers that were arrayed along the shoreline of the bay. In this article, we report the relocation rates (proportion of radio-tagged crabs that were recognized by at least one receiver) from that study because of their relevance to the assumption that tagging does not affect spawning behavior.

An important application of abundance estimates is in the calculation of harvest rates. We calculated harvest rates by dividing estimated abundance into 1) reported landings and 2) projected landings (based on recent regulations). The population that spawns in Delaware Bay disperses widely, some leaving the bay for the ocean. Calculations of harvest rate need to account for these migration patterns because landings from New Jersey and Delaware do not include landings of Delaware Bay spawning animals that were harvested in neighboring states (Virginia and Maryland). However, landings from neighboring states include animals that spawn in embayments other than Delaware Bay. Thus, use of landings from Delaware Bay states alone could underestimate harvest rate and use of landings from Delaware Bay and neighboring states could overestimate harvest rate. To put bounds on the problem, we calculated harvest rate 1) using landings from New Jersey and Delaware and 2) using landings from the Delaware Bay regional states (New Jersey, Delaware, Virginia, and Maryland).

Results

A total of 5398 males and 1823 females were tagged during the preseason period (26 March to 8 May 2003), and 7091 males and 3231 females were tagged during the prepeak period (28 to 30 May 2003; Table 1). Animals that were injured during capture were culled and not tagged. Culling rates were 0.19 during the preseason period, 0.05 during the prepeak period, and 0.12 overall.

During the spawning survey 22,051 males and 6675 females were counted in quadrats and examined for tags. Forty-eight tagged animals were recaptured during the spawning season surveys conducted 29 May, 31 May, and 2 June 2003. Nineteen of the recaptures were within quadrats, and 29 were between quadrats. Only three of the recaptured tags were from females. This number is not surprising; tags are difficult to detect on females because the females remain buried during spawning. The between-quadrat recaptures were not used in the estimation because we did not have a corresponding count of unmarked animals.

Using the Petersen estimator and all releases, we estimated that there were approximately 14.5 million (SE=3.2 million) adult male horseshoe crabs in Delaware Bay during peak spawning at the end of May 2003. Using just the prepeak releases, we estimated 13 million adult males (SE=3.6 million).

Model comparisons indicated that recapture probabilities were time-specific, but the temporary effect on recapture probabilities was not supported by the data (Table 2). The maximum likelihood estimate of male abundance with model 2 (Table 2) was 16.1 million (90% CI: 9.9 to 22.3 million). The difference between the Petersen estimate and the maximum likelihood estimate could have been due to model 2 that allowed for time-specific recapture probabilities, whereas the Petersen estimator did not. The maximum likelihood estimate based on constant recapture probabilities (i.e., model 1 in Table 2), matched the Petersen estimate (14.7 million for model 1 and 14.5 million for the Petersen estimate).

Sex ratios were different for the preseason and prepeak spawning periods in a pattern consistent with a sex-specific migration schedule. There was a smaller proportion of adult females in the bay during the preseason period (0.25) than when spawning activity was near its peak (0.31), which is consistent with the known observation that males migrate earlier than females. Sex ratios observed during the prepeak period were used to estimate abundance in the bay during the peak spawning period.

The assumption of equal catchability of tagged and untagged animals is an important assumption that af-

Table 1

Mark-recapture statistics for tagged horseshoe crabs (*Limulus polyphemus*) released during a prespawning season period (26 March to 8 May 2003) and a prepeak-spawning period (28 to 30 May 2003) and recaptured during spawning surveys on 29 May, 31 May, and 2 June 2003. M_{1s} is the number tagged preseason and M_{2s} is the number tagged before the peak at the time of the survey date (i.e., occasion s); u_s is the number of untagged that were counted during the survey; and m_{1s} is the number of prespawning season crabs recaptured and m_{2s} is the number of prepeak-spawning period crabs recaptured during the survey. Number untagged along the survey portion of the beach (u_s^*) was estimated from quadrat counts, i.e., [*number untagged on beach* = *beach length* (m) × *mean number per quadrat* (no./m^{-2}) – *number recaptured on beach*]. Survey portion of the beach was less than 1 km.

						Along beach			Quadrats		
Sex	Location	s	Survey date	M_1	M_2	u_s^*	m_{1s}	m_{2s}	u	m_{1s}	m_{2s}
Males	Baywide	1	29 May	5398	4828	55,750	3	4	6846	1	2
		2	31 May	5398	7091	48,498	10	6	5117	2	1
		3	2 June	5398	7091	96,718	10	12	10,088	4	8
	New Jersey	1	29 May	1448	3703	25,123	0	4	3890	0	2
		2	31 May	1448	5254	16,376	3	6	2113	1	1
		3	2 June	1448	5254	29,630	0	9	3524	0	6
	Delaware	1	29 May	3950	1132	30,631	2	0	2956	1	0
		2	31 May	3950	1837	32,129	7	0	3004	1	0
		3	2 June	3950	1837	67,099	10	3	6564	4	2
Females	Baywide	1	29 May	1823	2143	18,224	0	0	2149	0	0
		2	31 May	1823	3231	17,022	1	1	1712	0	0
		3	2 June	1823	3231	27,339	0	1	2814	0	1
	New Jersey	1	29 May	488	1567	8021	0	0	1169	0	0
		2	31 May	488	2268	3993	0	1	532	0	0
		3	2 June	488	2268	6859	0	0	809	0	0
	Delaware	1	29 May	1335	576	10,202	0	0	980	0	0
		2	31 May	1335	963	13,029	1	0	1180	0	0
		3	2 June	1335	963	20,480	0	1	2005	0	1

Table 2

Comparison between three likelihood-based models for mark and recapture of horseshoe crabs (*Limulus polyphemus*). Each model allowed a differed pattern of variation in recapture probabilities. The models are listed in order from least to most complex. In model 1, the recapture probabilities were set to be constant for both release cohorts (prespawning season period and prepeak-spawning period) and for all three recapture occasions. Model 2 allowed recapture probabilities to be time-specific, but equal for release cohorts. Model 3 allowed recapture to be time and cohort specific. Lower values for Akaikie information criteria (AIC) and ΔAIC indicate a better model fit; ΔAIC = 0 is the best fitting model. Likelihood ratio test (LRT) compares two nested models, and a significant P-value indicates the more complex model is supported.

				Likelihood ratio test	
Model	Variation in recapture probabilities	AIC	ΔAIC	Models compared	P-value
1	Constant	−348512.08	1713	Models 1 and 2	<0.0001
2	Time-specific	−350225.72	0	Models 2 and 3	0.77
3	Time and cohort-specific	−350220.83	5		

fects the accuracy of abundance estimates. Therefore, it was important to evaluate thoroughly whether tagged animals had different catchability than untagged animals. We tested for a temporary delay in spawning by comparing relative risk of recapture among the two release periods and by fitting a likelihood model that incorporated separate recapture probabilities for each release cohort (Table 2). Evidence did not support the hypothesis that initial capture and tagging temporarily affected spawning behavior (χ^2=2.03, df =2, P=0.36). The difference between the two release periods in the risk of being recaptured during peak spawning was

Table 3

Maximum likelihood estimates of abundance for adult horseshoe crabs (*Limulus polyphemus*) in Delaware Bay during the end of May 2003. Estimates of females and for both sexes combined ("Total") are based on mark-recapture estimates of males and sex ratios among the animals caught and released for this study. Adjusted estimates take into account the possible effect of capture on spawning by reducing releases of males by 0.88, which is an observed relocation rate for radio-tagged males.

	Maximum likelihood estimates		Adjusted estimates based on relocation rates from radio-tagged males	
	Abundance	90% CI	Abundance	90% CI
Males	16,140,000	9,910,000–22,300,000	13,730,000	8,780,000–19,400,000
Females	7,350,000	4,520,000–10,160,000	6,250,000	4,000,000–8,840,000
Total	23,490,000	14,430,000–32,460,000	19,980,000	12,7800,000–28,240,000

0.001 (90%CI: −0.0007 to 0.003). A model comparison test (likelihood ratio test in Table 2) did not support cohort-specific recapture probabilities (P=0.77). Although the difference in relative risk was in the direction of a temporary delay in spawning, the difference in recapture probabilities tended to be in the opposite direction. On two out of the three recapture occasions, the prepeak release cohort had a higher recapture probability than the preseason cohort. The maximum likelihood estimate of abundance of males with the use of model 2 (Table 2) was 20% higher for all releases (16.1 million crabs) than for prepeak releases only (13.4 million). A temporary delay in spawning would tend to cause abundance estimates based on late-releases to be higher than estimates including early releases, but in fact the opposite occurred. Thus, based on three lines of evidence, it is unlikely that there was a temporary delay in spawning due to the capture and tagging of males.

Another way in which tagged animals may behave differently from untagged animals is that tagged animals may forego spawning altogether. In 2004, we radio tagged horseshoe crabs using the same capture process that was used to tag animals in 2003. The radio-tagged horseshoe crabs were detected by radio receivers at high tide when the radio-tagged crabs emerged from the water to spawn. An array of fixed station receivers ensured nearly complete coverage of spawning habitat in Delaware Bay. Among radio-tagged males, we observed that age-specific relocation rates were 0.44, 1.00, and 0.74 for young, middle, and old-aged males, respectively. The frequencies of these age groups in the end of May 2003 tag releases were 0.07, 0.62, 0.31 for young, middle, and old-aged males. Thus, the average relocation rate predicted for the 2003 releases would be 0.88 (i.e., 0.44×0.07+1×0.62+0.74×0.31=0.88). There are several reasons for a failure to detect radio-tagged animals, namely behavioral response, movement beyond the range of radio receivers, transmitter loss or failure, and animal mortality. It is also possible that some adults migrate but do not spawn in a given year. Nevertheless, to be conservative, we adjusted the tag releases by the observed relocation rate (0.88) and computed estimates using the reduced releases. The 12% reduction in releases resulted in a 15% reduction in the abundance estimates (Table 3). From currently available estimates of fecundity (88,000 eggs per female; Shuster and Botton, 1985), we estimated that egg production in 2003 was 5.5×10^{11} (90% CI: 3.5×10^{11} to 7.7×10^{11}).

The adjusted estimates of abundance were 13.7 million (90% CI: 8.8 to 19.4 million) for males and 6.25 million (90% CI: 4.0–8.8 million) for females (Table 3). Landings in New Jersey and Delaware during 2003 were 2.4% (90% CI: 2–4%) of abundance estimates (Table 4). When landings from Virginia and Maryland are included, landings during 2003 were 4% (90% CI: 3–6%) of abundance. Harvest rates were similar for males and females because the sex ratio in the landings was similar to the ratio observed in our fishery-independent catch. We believe that our fishery-independent catch was a representative sample of mature animals in the bay.

We caught horseshoe crabs prior to and during the spawning migration. Thus, a comparison of pre- and postmigration catches could indicate the proportion of the population that over-wintered in the bay. We caught, on average, 18 adults per 15-min. tow on a vessel with two 2.3-m dredges from 25 March to 3 April 2003 prior to the spawning migration, which appeared to begin in mid-April. The catch-per-tow was 39 adults per tow during the period from 13 April to 8 May 2003 and 60 adults per tow during 28 to 30 May 2003. Thus, we were catching approximately one third (18/60=0.3) of the animals prior to spawning migration; this fraction could represent the proportion of the population that over-wintered in the bay and that did not migrate to the ocean between 2002 and 2003.

Discussion

There have been few attempts to estimate abundance of adult horseshoe crabs in Delaware Bay during the spawning run when the population is spatially concentrated. Shuster and Botton (1985) estimated population size from surveys on Delaware Bay beaches. However, a large portion of the bay was not included in the target

Table 4

Harvest rates calculated from 2003 landings and abundance estimates of adult horseshoe crabs (*Limulus polyphemus*) in Delaware Bay at the end of May 2003. To be conservative, estimates were adjusted according to the observed relocation rate (0.88) for radio-tagged male animals (see Table 3). NJ=New Jersey; DE=Delaware; VA=Virginia; and MD=Maryland.

	Delaware Bay (NJ and DE)			Delaware Bay Region (NJ,DE,VA,MD)
	Males	Females	Total	Total
Landings[1]	318,400	151,900	470,300	745,800
Abundance	13,700,000	6,250,000	19,980,000	19,980,000
	8.8 to 19 mil	4.0 to 8.8 mil	12.8 to 28 mil	12.8 to 28 mil
Harvest rate	0.023	0.024	0.024	0.04
	0.02 to 0.04	0.02 to 0.04	0.02 to 0.04	0.03 to 0.06

[1] ASMFC (Atlantic States Marine Fisheries Commission). 2004. 2003 Review of the fishery management plan for horseshoe crab (*Limulus polyphemus*), 13 p. ASMFC, 1444 Eye Street, NW, Sixth Floor, Washington, D.C. 20005

population study and was excluded from the survey. Carmichael et al. (2003) used transects located on a grid and visual counts in a shallow clear-water estuary to estimate abundance of the population in Pleasant Bay, Cape Cod, Massachusetts. Other estimates of the Delaware Bay population have been based on offshore surveys during nonspawning periods when populations are dispersed and possibly mixed (Botton and Haskin, 1984; Botton and Ropes, 1987; Hata and Berkson, 2003). Our mark-recapture estimates apply to adult horseshoe crabs present in Delaware Bay during late May 2003 when spawning peaked.

In previous horseshoe crab population estimates that were based on offshore surveys (Botton and Haskin, 1984; Botton and Ropes, 1987; Hata and Berkson, 2003), capture efficiency was unknown, and adults that remained in estuaries (i.e., those that did not migrate to the ocean after spawning) were not sampled. Hata and Berkson (2003) concluded that the capture efficiency for their trawl survey was intermediate between that of the trawl survey reported in Botton and Haskin (1984) and that of the hydraulic dredge survey reported in Botton and Ropes (1987). The most recent estimate of offshore abundance of 7.1 million crabs was reported by Hata and Berkson (2003). Botton and Haskin (1984) reported densities that were 1.8 to 2.9 times the densities reported by Hata and Berkson (2003), which would indicate a population estimate of 12 to 20 million according to the data of Botton and Haskin (1984). Botton and Ropes (1987) reported a minimum population of 2.3 to 4.1 million. The proportion of adults that remain in the Delaware Bay and do not migrate to the continental shelf after spawning is unknown. However, if the proportion of nonmigratory adults is sizeable (e.g., on the order of 0.3, which was indicated by our fishery-independent catches) then that, along with gear inefficiencies in trawl surveys, could explain the difference between the estimates in our present study and those of Hata and Berkson (2003).

Bias due to assumption violation is another reason for differences in estimates. We designed our study to obtain a representative sample when horseshoe crabs were concentrated and to minimize the time between release and recapture periods so that only a few days separated the prepeak release and recapture occasions. We released 17,543 tagged horseshoe crabs over two periods and examined 28,738 horseshoe crabs for tags, counting them in quadrats during subsequent spawning surveys (29 May, 31 May, and 2 June 2003). Low recapture rates (<1%) were consistent with a large population. However, it was important to evaluate the potential effects of assumption violations. Tag loss and tag-induced mortality were likely to be trivial because of the short period during which crabs were at large and results from field studies and laboratory experiments have shown no tag loss or tag-induced mortality (Crawford[3]; Brousseau et al., 2004). Brousseau et al. (2004) attached combined acoustic and radio tags and standard button tags to 24 female horseshoe crabs along two beaches in Delaware Bay, and then tracked them for eight days. All 24 were detected at least once, and 20 spawned on the beach of release within eight days of release, indicating that handling and tagging had a minimal effect on spawning behavior. Tags could have been overlooked during the spawning survey, which is why we limited our analysis to males counted and recaptured within 1-m^2 quadrats.

We evaluated the effect of capture and tagging on spawning behavior, and found no evidence that tagged males delayed spawning. Using radio-tagged horseshoe crabs, we believe it is possible that tagged crabs terminated spawning, and we adjusted abundance estimates based on relocation rates of radio-tagged crabs. Thus, we based our inference on abundance estimates that were adjusted downward to account for that possibility.

Recapture rates were low over the short time period for our study. However, annual recapture rate was approximately 4% for all tag releases and recaptures.

Mark-recapture studies have been frequently applied to marine species for describing migration or estimating mortality (Hoenig et al., 1998; Bacheler et al., 2005). Mark-recapture methods are used infrequently for abundance estimates of marine species, with the exception of anadromous species, whose spawning migration concentrates the population and enhances opportunities for recapture (Schwarz and Taylor, 1998). Similarly, the unusual horseshoe crab spawning migration and behavior concentrated the population and made them assessable for recapture. The validity of our abundance estimates is founded on a large number of tag releases and animals checked for tags, a study design that ensured population closure, an adequate number of samples to represent the population, and an evaluation of the underlying assumptions.

The sex ratio in our fishery-independent catch (69% M: 31% F), which we believe is a representative sample of adults in the bay at the time of peak spawning, was similar to the sex ratio in the landings (68% M: 32% F). Hata and Berkson (2003) observed a similar sex ratio among adults in an offshore trawl survey (63% M: 37% F). Although, commercial landings in 2003 were not skewed toward the harvest of females, harvest could have selected females disproportionately in past years.

The horseshoe crab harvest has been reduced through a series of reductions mandated by ASMFC (ASMFC[4]). Although there is evidence of stock decline coincident with increased landings in the past 10–20 years (ASMFC[4]), the estimates presented in the present study indicate recent regulatory changes had achieved a low harvest level by 2003. Based on the abundance estimates reported here, harvest rate in 2003 was 0.024 (90% CI: 0.02 to 0.04) for Delaware Bay state landings and 0.04 (90% CI: 0.03 to 0.06) for Delaware Bay area landings. In 2004, additional regulations were enacted, which capped landings at 150,000 per state for Delaware and New Jersey and prohibited harvest during May and early June when migrant shorebirds stopover in Delaware Bay. As a result of the 2004 regulations, landings dropped to 173,023 (males and females) for Delaware and New Jersey combined, which is a 63% drop from 2003 landings. Sex ratio of the 2004 landings was 68% M: 32% F, consistent with the 2003 landings.

Estimating abundance is an important step in the process of determining the current capacity for horseshoe crab egg production in the bay and for managing for the energetic needs of shorebirds. We estimate that egg production in 2003 was 5.5×10^{11} (90% CI: 3.5×10^{11} to 7.7×10^{11}). The U. S. Fish and Wildlife Service Shorebird Technical Committee (USFWS[5]) estimated that a population of 423,000 shorebirds would require 1.07×10^{11} horseshoe crab eggs as they migrated through Delaware Bay. This represents approximately 20% of all egg production, which would have to be available temporally and spatially during the shorebird migration.

Egg availability for shorebirds will depend also on overlap between horseshoe crab and shorebird migrations, density-dependent bioturbation, and wave-mediated vertical transport. Some important aspects of egg production and the process of making eggs available to foraging shorebirds are not well understood and have not been quantified. For example, if fecundity is found to be age- or size-related, then age or size would need to be incorporated in a calculation of egg abundance. Also, the process of bioturbation, which releases buried eggs to the beach surface, is known to be related to the density of spawning females, but has not been parameterized (Jackson et al., 2002). Determination of the dietary requirements of migrant shorebirds in terms of horseshoe crab eggs coupled with reliable estimates of abundance, fecundity, and bioturbation rates, will set the stage for a management of horseshoe crabs that takes into account the trophic support it provides in Delaware Bay.

[4] ASMFC (Atlantic States Marine Fisheries Commission). 2004. Horseshoe crab 2004 stock assessment report, 87 p. ASMFC, 1444 Eye Street, NW, Sixth Floor, Washington, DC 20005.

[5] USFWS (United States Fish and Wildlife Service). 2003. Delaware Bay shorebird-horseshoe crab assessment report and peer review. U.S. Fish and Wildlife Service Migratory Bird Publication R9-03/02, 99 p. USFWS, 4401 N. Fairfax Drive, Arlington, VA 22203.

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Estimates of commercial longline selectivity for Pacific halibut (*Hippoglossus stenolepis*) from multiple marking experiments

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The term "selectivity" refers to the relationship between the size (or age) of a fish and its vulnerability to a given kind of fishing gear. A selectivity schedule, along with other parameters, is normally estimated in the course of fitting a stock assessment model, and the estimated schedule can have a large effect on both the estimate of present stock abundance and the choice of an appropriate harvest rate. The form of the relationship is usually not known and not well determined by the data, and equally good model fits can often be obtained with different plausible specifications of selectivity. Choosing among the model fits and associated abundance estimates in this situation is problematic (Sigler, 1999; Sullivan et al., 1999).

The selectivities of different gears can be compared by fishing the gears side by side, but without knowing the size composition of the stock being fished, it is impossible to determine the form of the selectivity functions. Therefore, one has to make some assumptions about them in order to locate estimates (Millar and Fryer, 1999, and references therein). In this case, too, equally good fits can often be obtained with a variety of assumed forms (Huse et al., 2000; Woll et al., 2001); therefore the true form cannot be determined by simple fishing experiments.

Mark-recapture data can yield direct and reliable estimates of selectivity because in this situation the size composition of the fished stock is known (Myers and Hoenig, 1997). In this note, we report estimates of the commercial longline selectivity of Pacific halibut (*Hippoglossus stenolepis*) based on the large number of mark-recapture experiments conducted by the International Pacific Halibut Commission (IPHC) in the 1960s, 1970s, and 1980s. A similar analysis was done by Myhre (1969), but he used data from only two experiments; the present study uses data from more than 100 experiments.

Materials and methods

Kaimmer (2000) described all IPHC tag data for all varieties of external tags in setline and trawl catches dating back to 1925. We also used tag data for all varieties of tags (except the small strap type); however, our data were for tags released during setline catches only and our data dated back to 1960, the first year of recorded data in the computer release and recovery IPHC database. The total number of tags released was over 100,000, of which more than 13,000 were recovered in the commercial longline fishery. About half of the releases were at systematically placed setline survey stations that covered a large part of an IPHC regulatory area (Fig. 1). The other half were at "spot" fishing locations, deliberately chosen to produce good catches, either for marking or for gathering data on the performance of different gear types. For our study, an experiment was defined as all releases of a given tag type in a given regulatory area in a given year during either survey or spot fishing operations (not both), where at least 10 fish were released. Between 1960 and 1990 there were 131 such experiments.

These data are not usable for estimating exploitation rates or migration rates because of uncertainty concerning things like recovery effort and reporting rates, but they can be used to estimate commercial selectivity. In the case of a single experiment, a straightforward plot of short-term recovery rate by length at release will show how selectivity changes with length. The absolute recovery rates will depend on usually unknown factors (tagging, fishing, and natural mortality rates; tag loss and reporting rates), but the relative recovery rates should depend mainly on selectivity (barring large variations in length with any of the unknown factors).

Myers and Hoenig (1997) showed how data from many experiments can be combined to obtain a single set of selectivity estimates. To summarize their derivation, let $\pi_{i,l}$ be the recovery rate of fish of length l in experiment i. This rate is treated as the product of a length-specific commercial selectivity s_l, which is the same for all experiments, and an experiment-specific recovery rate r_i that combines all the unknown factors mentioned above. Thus $\pi_{i,l}=r_i \cdot s_l$ and $\log\pi_{i,l}=\log r_i+\log s_l$. This has the form of a generalized linear model with a log link function and a binomial variance; therefore the point and variance estimates can be obtained in standard fashion.

Some rule has to be chosen for scaling the selectivities to make the model determinate. The most common rule is to require that the maximum selectivity be 1.0, but that can involve using a scaling factor that is poorly determined by the data if the maximum occurs in a length group with few releases and recoveries. To avoid this problem, the rule used in

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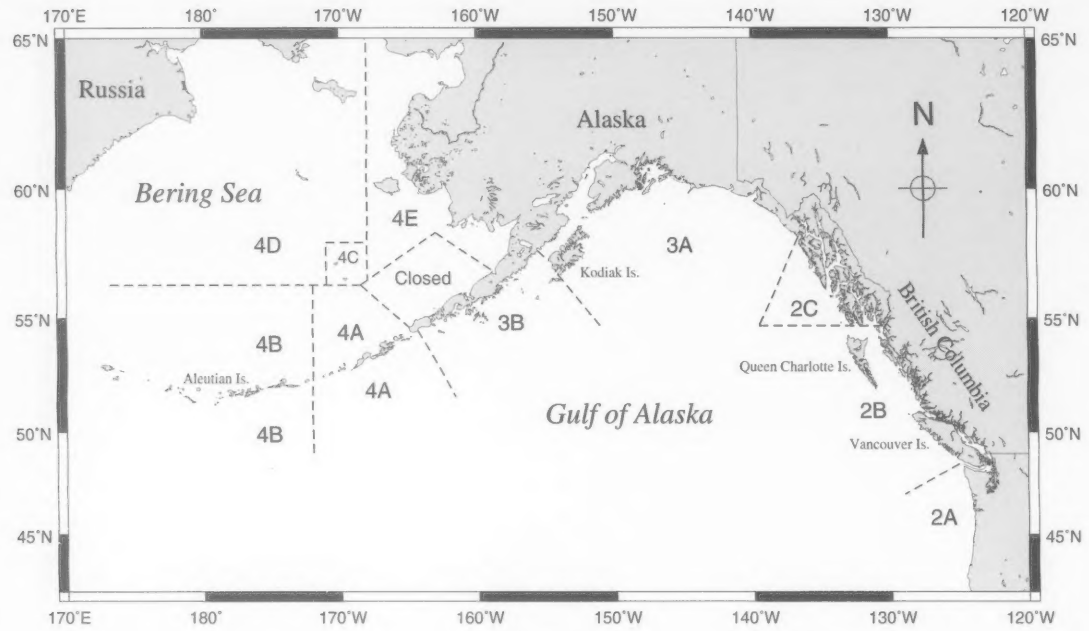

Figure 1

International Pacific Halibut Commission regulatory areas. The area marked "closed" is permanently closed to directed halibut fishing.

our study was to define selectivity to be 1.0 at 120 cm. Estimated selectivity could therefore exceed 1.0 at other lengths.

Results

Figure 2 shows the estimates of commercial length-specific selectivity in areas 2B, 2C, 3A, and 3B obtained by the method of Myers and Hoenig (1997) with the use of all available data in each area. There were insufficient data in area 4 to calculate useful estimates. The estimates in Figure 2 were calculated by using all recoveries from each release during the first two years at liberty, including recoveries from outside the release area and recoveries from unknown locations. Estimates computed by using only recoveries from the area of release were no different from those obtained by using all of the recoveries.

In all areas, commercial selectivity in the period of 1960–90 appears to increase with length up to a maximum and then decline. In area 2B, the peak occurs at about 110 cm and there is a substantial decline thereafter, to around half the peak value. In Alaska (areas 2C, 3A, 3B), selectivity peaks at a much larger size (about 150 cm). Thereafter the decline is about as steep as in area 2B, but not as large because so little of the length composition remains beyond 150 cm.

Recoveries from releases at spot fishing locations show a selectivity pattern similar to that for the entire dataset. The same is true of survey releases, except in area 2B where the selectivity pattern does not show a decline among larger fish. But this impression depends on a small number of recoveries, and therefore it may be false.

Discussion

In previous modeling of length-specific selectivity, the IPHC staff generally assumed some kind of asymptotic function, with full selection occurring at 110–130 cm. A function of this form is consistent with video observations of halibut behavior when they are hooked (Kaimmer, 1999), and it produces satisfactory fits to the observed length compositions of survey and commercial setline catches in the annual stock assessment. It is also consistent with the conventional view that hook selectivity varies little with size among fish large enough to take the bait (Lokkeborg and Bjordal, 1992). But the large body of mark-recapture data shows a different pattern: selectivity declining after the peak at 110 cm in area 2B, and not reaching a peak until 150 cm or so in Alaska. These patterns are, in fact, quite similar to those reported by Myhre (1969).

Commercial fishing selectivity reflects ground selection by the fleet, as well as size selection by the gear. It is therefore possible that the selectivity of commercial setline gear on a given ground has the expected asymptotic form, but ground selection has the effect of

targeting certain size groups and thereby producing a different selectivity schedule. In area 2B, for example, the best catch rates may be achieved by targeting smaller fish; whereas in Alaska it may be more profitable to target larger fish.

If the decline in selectivity in area 2B were the result of the commercial fishery targeting areas where the fish are smaller, one would expect to see the decline in data from survey releases (which are done over the whole area), but not in data from releases at spot fishing locations (most of which are customary commercial fishing locations). However, the mark-recapture data show the opposite pattern, if anything; therefore ground selection does not appear to be the explanation.

When length-specific selectivity is allowed to be dome-shaped in the stock assessment model (rather than forced to be asymptotic), the estimated commercial selectivities turn out to be quite similar in pattern to the mark-recapture estimates, including the differences among areas. But the selectivities estimated for the IPHC systematic setline survey are asymptotic or ramp-shaped, rather than dome-shaped. They indicate that ground selection by the commercial fishery really does have an effect on the form of commercial selectivity, contrary to what the mark-recapture data may indicate.

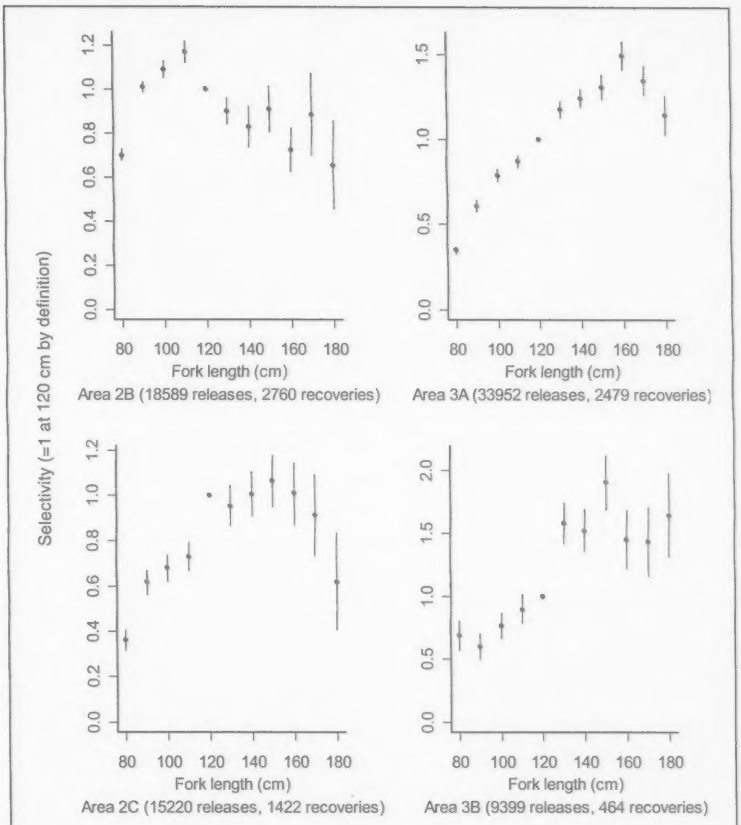
Selectivity (=1 at 120 cm by definition)
Fork length (cm)
Area 2B (18589 releases, 2760 recoveries)
Area 3A (33952 releases, 2479 recoveries)
Area 2C (15220 releases, 1422 recoveries)
Area 3B (9399 releases, 464 recoveries)

Figure 2

Estimates of length-specific commercial selectivity (±1 standard deviation) for Pacific halibut (*Hippoglossus stenolepis*) based on all releases 1960–90, by regulatory area. The scale was set by defining selectivity to be 1.0 at 120 cm, so that value has no standard deviation, and other values can and do exceed 1.0.

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Hatching date, nursery grounds, and early growth of juvenile walleye pollock (*Theragra chalcogramma*) off northern Japan*

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Walleye pollock (*Theragra chalcogramma*) is widely distributed in the North Pacific Ocean and plays an important role in coastal subarctic ecosystems. The Japanese Pacific population of this species is one of the most important demersal fishes for commercial fisheries in northern Japan. The population is distributed along the Pacific coast of Hokkaido and the Tohoku area (Fig. 1), which is the southern limit of distribution of the species in the western North Pacific. In Funka Bay, the main spawning ground for this population, pollock spawn from December to March (Kendall and Nakatani, 1992). Planktonic eggs and larvae are transported into the bay, where juveniles usually remain until late July when they reach 60–85 mm in total length (Hayashi et al., 1968; Nakatani and Maeda, 1987). These juvenile pollock then migrate from Funka Bay eastward to the Doto area off southeastern Hokkaido (Honda et al., 2004). Many studies on eggs, larvae, and juveniles of the species have been conducted in or near Funka Bay, but little information is available on the ecology of the early life stages in the Tohoku area. Hashimoto and Ishito (1991) suggested that eggs are transported from Funka Bay southward to the Tohoku area by the coastal branch of the Oyashio Current, but there has been no study to verify this hypothesis.

The aim of the present study was to examine, by using otolith daily growth ring analysis, regional differences in hatching date, body size, and early growth of juvenile pollock in Funka Bay and the Tohoku area and to elucidate the importance of Tohoku area as a nursery ground for the Japanese Pacific population of pollock.

Materials and methods

The present study was carried out from Funka Bay to the Tohoku area. We divided the study area into four regions, Funka Bay, east of Tsugaru Strait, northern Tohoku, and southern Tohoku (Fig. 1). East of Tsugaru Strait region is located between Funka Bay and the Tohoku area. Sampling was done at a total of 54 stations mostly in late May during three years, from 1999 to 2001: 10 for 1999, 23 for 2000, and 21 for 2001 (Table 1). In Funka Bay, sampling stations were set up only at the bay mouth area because there was a lot of fishing gear inside the bay. Pollock juveniles were collected with a midwater trawl (NST-92-K1, Nichimo Co., Ltd., Shinagawa, Tokyo) onboard the RV *Wakataka Maru* of the Tohoku National Fisheries Research Institute (TNFRI).

The midwater trawl, which had a round mouth opening with a diameter of about 20 m, was towed only during the day. The overall length of the net was 98.3 m and it had a variable-size mesh of 14 m (stretched) in the forward section to 3 mm (square mesh) at the codend. All tows were made at an average ship speed of 4 knots. The horizontal tows were carried out in 1999, whereas the double oblique tows were made from the surface to near the bottom (10–20 m above the bottom) in 2000–2001. The sampling biases of the net were not investigated, but biases may have been neglible for two reasons. First, our net had a larger mouth opening than that of the Methot trawl (5 m^2) used for collecting late larval and early juvenile stages of walleye pollock (Brodeur et al., 1995). Second, we could sample juveniles that hatched from mid-December to mid-April in our survey and the juveniles were thought to be from eggs that spawned throughout the whole spawning season (December to March) in Funka Bay.

Pollock juveniles were sorted from the codend samples and preserved in 95% ethanol diluted with seawater for otolith daily-growth analysis. Total length (TL) of some pollock was measured to the nearest 0.1 mm on board the vessel, whereas the same length of preserved fish was similarly measured in the laboratory. The following formula was used to change TL of preserved fish to TL of fresh fish:

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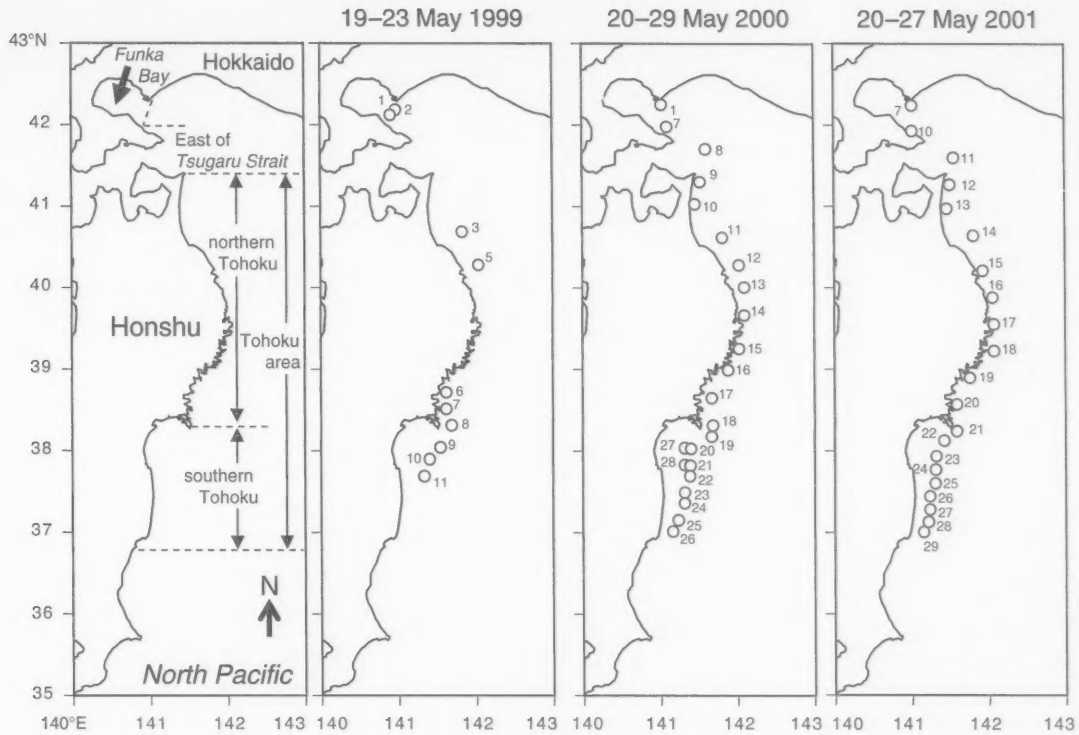

Figure 1

Sampling stations (open circles) for walleye pollock (*Theragra chalcogramma*) caught with a midwater trawl net in four regions off the Pacific coast of northern Japan in May 1999–2001. Arabic numerals indicate station numbers (see Table 1).

$$TL\ of\ fresh\ fish = 1.0126(TL\ of\ preserved\ fish) + 1.7934 \quad [n=97,\ r^2=0.974].$$

To study the daily otolith increment of our sample, we employed the methods established by Nishimura and Yamada (1984), Bailey and Stehr (1988), Yoklavich and Bailey (1990) and Bailey et al. (1996). Sagittal otoliths, hereafter called "otoliths," from the juveniles were embedded in epoxy resin on glass slides and ground with carbon paper (no. 800–1200) perpendicularly to the otolith flat plane along the long axis (frontal section). Polished otoliths were selected if they included the otolith nucleus on the ground surface and were thin enough to transmit light under a light microscope. Then 1171 specimens were polished with lapping film, cleaned, and observed. Early narrow increments were counted under 600× or 1000× magnification. As the increments increased in width, the magnification was changed to 400×. Hatching date was estimated by subtracting the number of increments from the sampling date.

Daily growth-ring diameter is the index of body length at an age because a significant linear relationship exists between log-transformed body length and otolith length data for pollock juveniles (Nishimura and Yamada, 1988). In the present study, we measured the short otolith radius (SOR) along the long axis obtained from a frontal section and used the SOR from the nucleus to the 30th ring (SOR 30) as the index of early growth. SOR 30 was measured for the specimens collected in 2000, by using the otolith daily growth ring analyzing system (Ratoc System Engineering Co., Ltd., Shinjuku, Tokyo). The Mann-Whitney *U*-test was used to identify differences in SOR 30 groups. We were not able to use analysis of covariance (ANCOVA) because an interaction was found by analysis of variance (ANOVA) in size-at-age relationships among regions in 2000 ($P<0.0001$) and 2001 ($P=0.035$). Comparisons of specific growth rate (SGR) for the juveniles were made between our regions by the Mann-Whitney *U*-test or ANOVA. Comparisons of means were made using Scheffe's test. SGR values of individual fish were calculated by using the following formula (Ricker, 1979):

$$SGR = \frac{(\ln L_2 - \ln L_1)\times 100}{t_2 - t_1},$$

Table 1

Summary of midwater trawl surveys in May of 1999–2001. SST=sea surface temperature, OB= oblique tow, HZ=horizontal tow.

Station no.	Sampling date	Depth (m)	SST (°C)	Towing time (min)	Method	Number of fish	CPUE (fish/h)
1	19 May 1999	69	7.2	63	HZ	6	5.7
2	19 May 1999	69	7.2	70	HZ	129	110.6
3	21 May 1999	99	10.6	72	HZ	4	3.3
5	21 May 1999	108	10.7	84	HZ	19	13.6
6	23 May 1999	97	11.2	88	HZ	0	0
7	23 May 1999	124	11.8	74	HZ	0	0
8	23 May 1999	136	11.6	93	HZ	0	0
9	22 May 1999	106	14.7	98	HZ	0	0
10	22 May 1999	102	16.4	84	HZ	0	0
11	22 May 1999	100	17.1	49	HZ	0	0
1	20 May 2000	84	8.4	45	OB	730	973.3
7	21 May 2000	101	8.3	57	OB	173	182.1
8	21 May 2000	111	9.6	48	OB	399	498.8
9	21 May 2000	90	10.1	42	OB	0	0
10	22 May 2000	123	10.8	50	OB	6	7.2
11	22 May 2000	111	9.2	51	OB	17	20.0
12	22 May 2000	107	10.9	54	OB	69	76.7
13	25 May 2000	121	11.3	62	OB	90	87.1
14	25 May 2000	151	10.9	48	OB	14	17.5
15	25 May 2000	138	10.9	43	OB	163	227.4
16	26 May 2000	122	11.0	49	OB	57	69.8
17	26 May 2000	133	13.1	48	OB	81	101.3
18	26 May 2000	143	13.7	51	OB	24	28.2
19	26 May 2000	121	14.3	51	OB	22	25.9
20	27 May 2000	104	12.5	48	OB	62	77.5
21	27 May 2000	122	13.7	48	OB	37	46.3
22	27 May 2000	130	12.8	57	OB	29	30.5
23	27 May 2000	97	12.5	44	OB	37	50.5
24	27 May 2000	105	12.9	51	OB	11	12.9
25	28 May 2000	77	9.7	60	OB	11	11.0
26	28 May 2000	102	9.9	50	OB	35	42.0
27	29 May 2000	69	13.3	47	OB	144	183.8
28	29 May 2000	82	12.6	45	OB	15	20.0
7	20 May 2001	71	10.2	55	OB	51	55.6
10	20 May 2001	103	7.6	39	OB	2371	3647.7
11	22 May 2001	117	10.4	48	OB	1	1.3
12	22 May 2001	90	11.0	40	OB	0	0
13	22 May 2001	176	10.5	48	OB	10	12.5
14	23 May 2001	109	10.3	51	OB	11	12.9
15	23 May 2001	104	10.6	52	OB	106	122.3
16	23 May 2001	120	13.1	45	OB	117	156.0
17	24 May 2001	141	11.7	60	OB	19	19.0
18	24 May 2001	147	11.5	44	OB	6	8.2
19	24 May 2001	108	10.7	23	OB	2	5.2
20	25 May 2001	130	10.5	31	OB	0	0
21	25 May 2001	115	11.2	23	OB	2	5.2
22	25 May 2001	112	11.6	45	OB	1	1.3
23	25 May 2001	104	12.0	22	OB	0	0
24	26 May 2001	120	13.4	42	OB	0	0
25	26 May 2001	125	12.0	57	OB	0	0
26	26 May 2001	97	12.1	35	OB	0	0
27	27 May 2001	106	15.7	35	OB	0	0
28	27 May 2001	100	19.1	52	OB	0	0
29	27 May 2001	103	19.6	21	OB	0	0

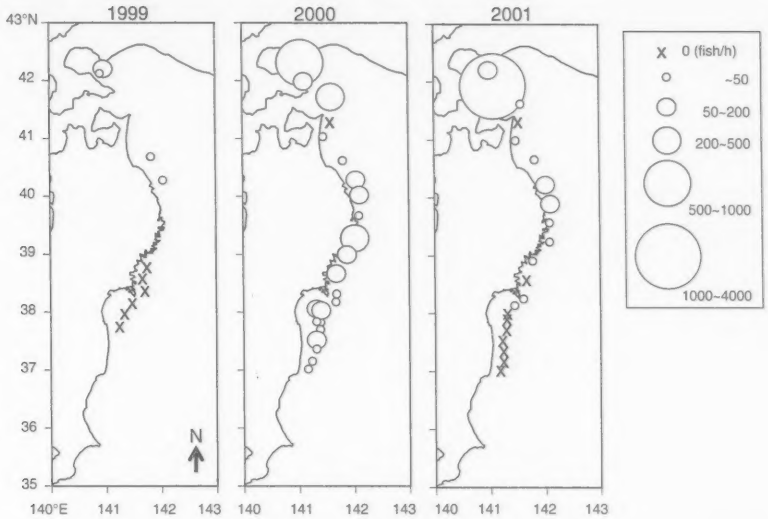

Figure 2

Distribution of catch per unit of effort (CPUE) (fish/hour) for walleye pollock (*Theragra chalcogramma*) caught with a midwater trawl net in May 1999–2001 off the Pacific coast of northern Japan.

where L_2 and L_1 = body length at time t_2 and t_1, respectively.

In this study, we defined L_1 = 4.6 mm at hatching (t_1=0) according to Nishimura and Yamada (1988) and L_2= TL of fish at the number of otolith increments (t_2). All tests were evaluated for significance at the P=0.05 level.

Results and discussion

Distribution of juveniles

In 1999, juvenile pollock were collected only from Funka Bay to northern Tohoku, but no fish were sampled in southern Tohoku (Fig. 2). In 2000, juvenile pollock were caught in abundance at almost all sampling stations: highest catch per unit of effort (CPUE) was recorded at a station in Funka Bay (973 fish/h) and many juveniles were found in northern and southern Tohoku (max: 227 and 184 fish/h, respectively). In 2001, the juvenile distribution was similar to that in the previous year, but few juveniles were caught in southern Tohoku. These results show interannual variability in the distribution of juvenile walleye pollock between 1999 and 2001.

Inada and Murakami (1993) suggested that the pollock catch and distribution in the Tohoku area are strongly affected by the coastal branch of the Oyashio Current but little information is available on the relationship between oceanographic conditions and juvenile distribution and abundance in this area. The southern limit of the coastal branch characterized by the position of 5°C at 100 m depth has been regarded as an index to show the strength of the current (Ogawa, 1989). Thus we examined annual changes in the position of southern limit of the coastal branch based on water temperature data (TNFRI[1]). In April, the coastal branch of the Oyashio Current mostly stagnated in northern Tohoku in 1999 and 2001 but there were some annual variations, but it went far south to southern Tohoku in 2000 (Fig. 3A). It is likely that the juvenile distribution in May of the three years from 1999 to 2001 is associated with the southern limit position of the coastal branch of the Oyashio Current in April. Kitagawa et al.[2] reported the recruitment index of age-0 pollock based on bottom trawl surveys in the Tohoku area. We compared the recruitment index (X, $\times 10^3$ fish) given by Kitagawa et al.[2] with the latitude of the southern limit of the coastal branch of the Oyashio Current (Y) and, as a result, a significant relationship was observed in the 1995–2001 data ($Y=46.653X^{-0.019}$, r^2=0.960, Fig. 3B). This result may indicate that abundant recruitment is brought by

[1] TNFRI (Tohoku National Fisheries Research Institute). 1997–2002. Tohoku Block Suisan Kaiyo Renraku Kaihou, vols. 26–32. TNFRI, Fisheries Oceanography Division, 3-27-5 Shinhama-cho, Shiogama, Miyagi 985-0001, Japan. [In Japanese.]

[2] Kitagawa, D., T. Hattori, and Y. Narimatsu. 2002. Monitoring on the demersal fish resources in the Tohoku area. *In* Kaiyo Monthly 34, p.793–798. Seikai Nat. Fish. Res. Inst., 1551-8 Taira-machi, Nagasaki, Nagasaki 851-2213, Japan. [In Japanese, the title was translated by the authors.]

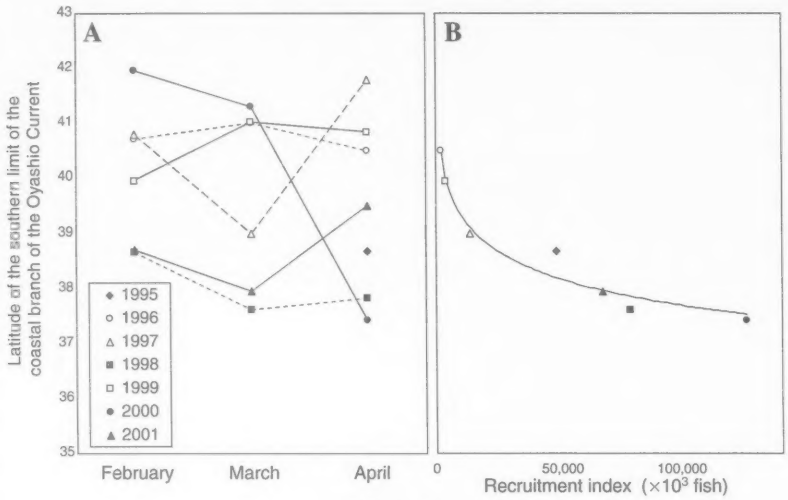

Figure 3

Monthly change in the latitude of the southern limit of the coastal branch of the Oyashio Current (**A**), and the relationship between recruitment index of age-0 walleye pollock (*Theragra chalcogramma*) in the Tohoku area and the latitude of the southern limit of the coastal branch of the Oyashio Current (**B**). This figure is drawn according to the water temperature data from the Fisheries Oceanography Division of the Tohoku National Fisheries Research Institute (TNFRI) (see text). The data on the recruitment index are from Kitagawa et al.[2] (see general text).

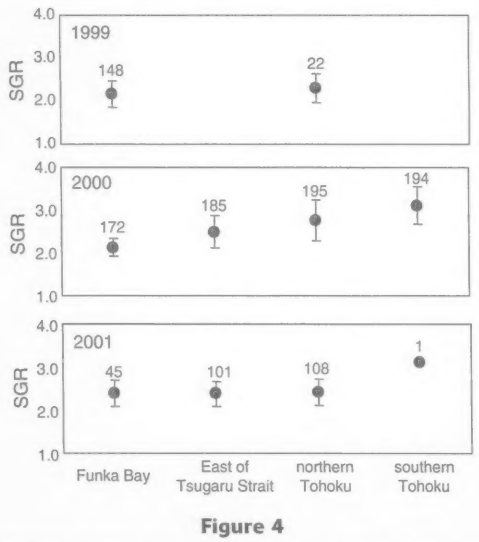

Figure 4

Specific growth rate (SGR) for walleye pollock (*Theragra chalcogramma*) from four regions off the Pacific coast of northern Japan in 1999–2001. Vertical bars indicate standard deviation and arabic numerals indicate number of samples.

a strong coastal branch of the Oyashio Current in the Tohoku area.

Early growth of walleye pollock

There was no difference in SGR between Funka Bay and northern Tohoku in 1999 (*U*-test, $P=0.111$, Fig. 4). Also, no regional differences were found among all regions in 2001 (ANOVA, $P=0.526$). For 2000, however, there were significant differences in SGR among all four regions (ANOVA, $P<0.0001$) and even between all pairs (Scheffe's test, $P<0.0001$).

In 2000, the SOR 30 values ranged from 30–58 μm for the juveniles collected in Funka Bay and east of Tsugaru Strait (Fig. 5). However, two different SOR 30 groups were found for the samples from northern and southern Tohoku (*U*-test, $P<0.0001$): one with SOR 30 values ranging from 30–60 μm and the other with values greater than 68 μm. Fish of the former group (low-growth group) had the same SOR 30 range as those from Funka Bay and east of Tsugaru Strait. The latter group (high-growth group) was observed only in the Tohoku area. Positive linear regressions were found in size-at-age relationships for low- and high-growth groups ($P<0.0001$, Fig. 6) and the difference of the SGR was significant between these two groups (*U*-test, $P<0.0001$).

These results indicate that the surveys of juvenile walleye pollock in May 2000 caught two growth groups:

the low-growth group that probably spawned in Funka Bay mixed with the high-growth group that was probably produced locally in the Tohoku area. This mixing of the two groups could have occurred primarily because of either advection or migration. Assuming that this interpretation is correct, it would be important for local fisheries managers to take account of these variations especially if the years of extra production from the Tohoku area expand the exploitable stock.

Length-frequency distribution and hatching date

The length-frequency distribution and hatching date composition for juvenile pollock among regions were similar in 1999 and 2001 but were different in 2000 (Figs. 7 and 8). In 2000, large fish over 40 mm TL, designated as forming part of the low-growth group, constituted the majority of the samples from Funka Bay, and much smaller fish of the same group (<40 mm TL) were widely distributed in waters from east of Tsugaru Strait to southern Tohoku. All juveniles from Funka Bay were categorized as low-growth group fish that hatched between late December and late February, and juveniles of the low-growth group that hatched after March 1 were caught widely from east of Tsugaru Strait to southern Tohoku in 2000. These results appear to indicate that late hatching fish originating from Funka Bay were transported to the Tohoku area by the strong coastal branch of the Oyashio Current after March 2000.

Nakatani and Sugimoto[3] showed that only fish hatching in January and February survived in Funka Bay in summer, whereas pollock usually spawn between December and March. Nakatani (1998) thus assumed that late hatching fish (after early March) would not be able to consume enough food during their settlement stage because the abundance of copepodids of *Pseudocalanus* spp., the main food for juveniles below 30 mm TL, decreases in late May and because late hatching fish cannot eat *Neocalanus plumchrus* due to its large size. Therefore, he suggested that there are two critical periods for walleye pollock during their early larval and settlement stages in Funka Bay. Considering these results, we suggest that when late hatching fish were transported to the Tohoku area, their survival rates were higher than those of juveniles that remained in Funka Bay.

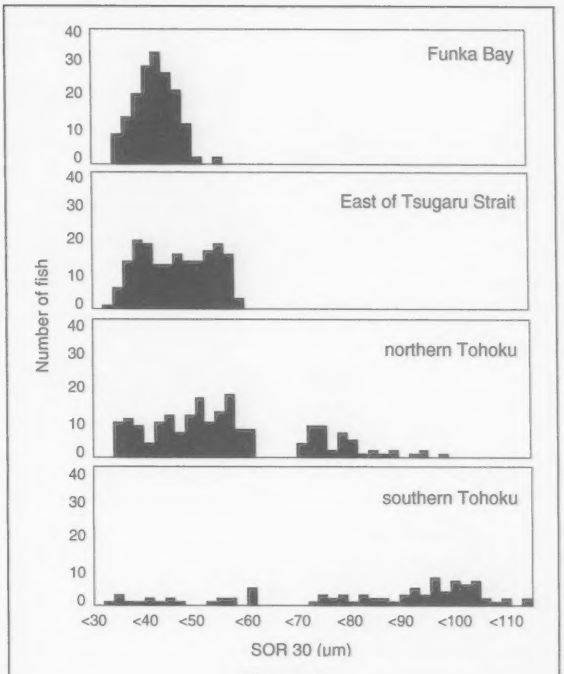

Figure 5

Frequency distribution of the short otolith radius from the nucleus to the 30th ring (SOR 30) for walleye pollock (*Theragra chalcogramma*) collected in four regions off the Pacific coast of northern Japan in 2000.

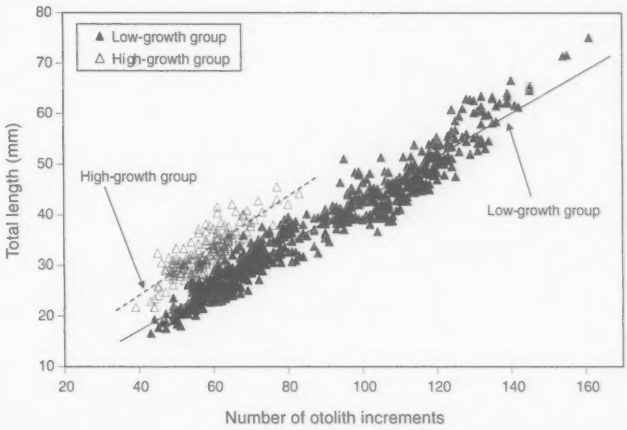

Figure 6

Size-at-age relationship for two growth groups of walleye pollock (*Theragra chalcogramma*) collected in 2000. Low- and high-growth groups were divided according to the SOR 30 distribution (see text and Fig. 5). The regression lines for each growth group are as follows: low-growth group: $TL=0.017+0.429\times age$ [$r^2=0.941$, $n=594$, $P<0.0001$]; high-growth group: $TL=4.694+0.486\times age$ [$r^2=0.715$, $n=152$, $P<0.0001$].

[3] Nakatani, T., and K. Sugimoto. 1998. Reproductive strategy of walleye pollock and the environment in the south region of Hokkaido, Pacific. *In* Kaiyo Monthly special vol., p.182–186. Graduate School of Fisheries Sciences, Hokkaido University, 3-1-1 Minato-cho, Hakodate, Hokkaido 041-8611, Japan. [In Japanese, the title was translated by the authors.]

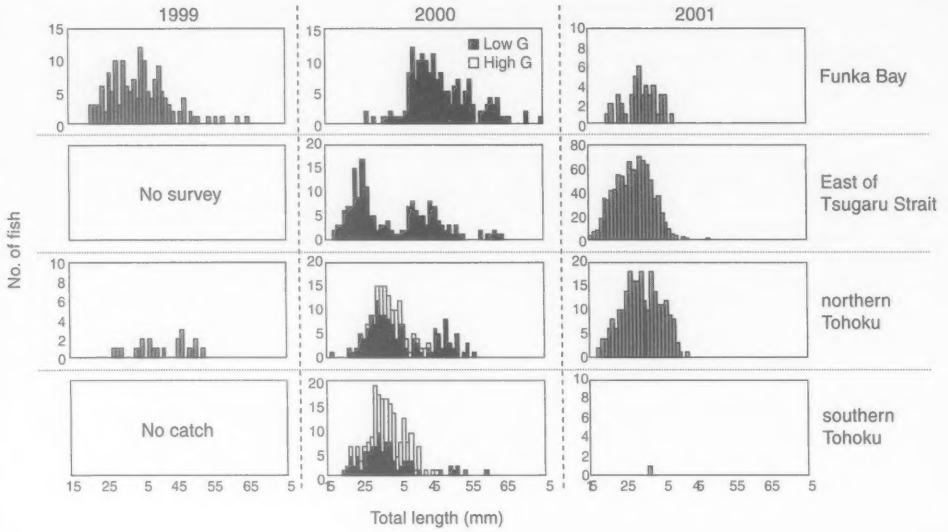

Figure 7

Total length-frequency distribution for walleye pollock (*Theragra chalcogramma*) from four regions off the Pacific coast of northern Japan in 1999–2001. Low G=low-growth group (solid bars); high G=high-growth group (open bars).

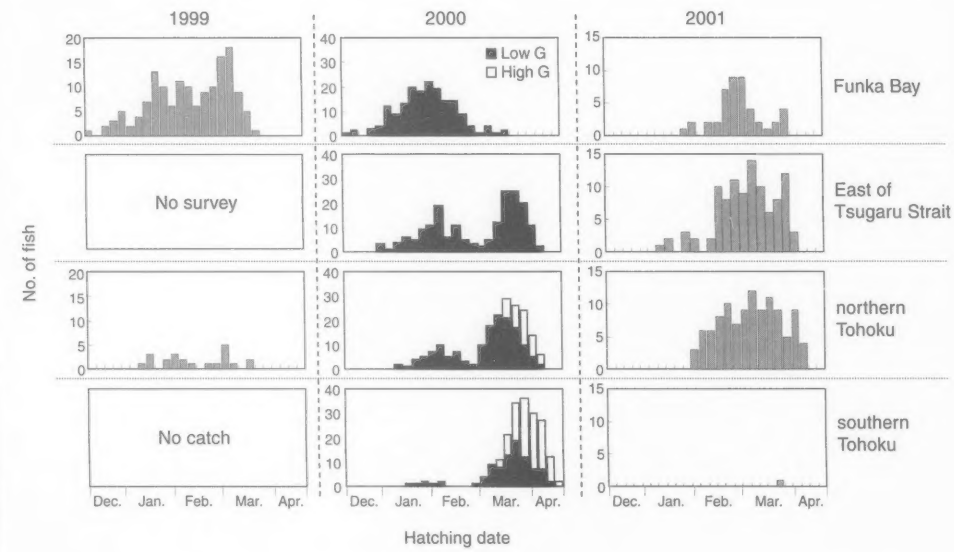

Figure 8

Hatching date composition for walleye pollock (*Theragra chalcogramma*) from four regions off the Pacific coast of northern Japan in 1999–2001. Low G=low-growth group (solid bars), high G=high-growth group (open bars).

We suggest that, in addition to the recruitment process in Funka Bay, an important recruitment process occasionally exists in the Tohoku area, and when the year-class strength of the Japanese Pacific population of pollock is strong, as in 2000 (Yabuki[4]), the Tohoku area becomes important as a nursery ground for the late hatching fish originating from Funka Bay.

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Development of larval and early juvenile penpoint gunnel (*Apodichthys flavidus*) (family: Pholidae)

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The penpoint gunnel (*Apodichthys flavidus*) is a member of the perciform family Pholidae. Pholids, commonly referred to as gunnels, are eel-like fishes that inhabit the rocky intertidal and subtidal regions of the northern oceans and are often associated with macroalgae, such as *Fucus* spp. or kelp (Watson, 1996). Gunnels are ecologically important forage fishes that form part of the diet of birds and commercially important groundfish species (Hobson and Sealy, 1985; NMFS[1]; Golet et al., 2000). The diet of *A. flavidus* and other pholids comprises primarily harpactacoid copepods, gammarid amphipods, isopods, and other crustaceans (Cross, 1981). *Apodichthys flavidus* ranges along the west coast of North America from southern California to the Gulf of Alaska (Mecklenburg et al., 2002). Adult *A. flavidus* are distinguished from other pholids by their total vertebral counts, the presence of a thick and grooved first anal spine, a preanal length that is approximately 60% standard length (SL), and a dark green to light olive coloration (Yatsu, 1981). It is one of the largest pholids (up to 46 cm) and is important in the live fish trade for both home and public aquaria (Froese and Pauly[2]).

In late winter to early spring months (January–April), adult *A. flavidus* spawn in nearshore waters. A single female lays clusters of demersal, adhesive eggs onto substrate that a male will guard until hatching (Clemens and Wilby, 1961; Wilkie, 1966; Marliave, 1975). The eggs are 3 mm in diameter and the incubation period is approximately 2.5 months (Wilkie, 1966; Marliave, 1975). Larvae are about 12–13 mm total length (TL) at the time of hatching, well developed, and have pigmented eyes, an elongated body, and very little to no yolk sac (Wilkie, 1966; Marliave, 1975). After about 50 days, the larvae settle as juveniles and are approximately 25 mm SL (Marliave, 1975). Although *A. flavidus* reproduction has been well-studied, there has not been a complete description of larval development. Wang[3] provided a summary of life history information and pencil illustrations of early flexion, postflexion, and juvenile stages. Matarese et al. (1989) published an illustration of a 15.0-mm flexion larva and some characters distinguishing *A. flavidus* from *Pholis* spp.

In the present study we describe development of *A. flavidus* from recently hatched larvae to newly settled juveniles, including some general aspects of osteological development. Larval *A. flavidus* are compared with larvae of other pholid species included in the genus *Apodichthys* by Yatsu (1981, 1985): *Xererpes fucorum* and *Ulvicola sanctaerosae*. This classification was not followed by Matarese et al. (1989) or Watson (1996) and is not followed in the present study. This work will aid in the accurate identification of *A. flavidus* larvae in samples taken during nearshore ichthyoplankton surveys and in ecological studies and will contribute to a better understanding of pholid systematics.

Materials and methods

We examined 58 larval and juvenile *A. flavidus* (11.9–42.3 mm) collected in dip-net surveys by scientists of the Alaska Fisheries Science Center (AFSC; Busby et al., 2000) and the University of Washington (UW) from four sites: Clam Bay (47°34.5′N, 122°32.5′W), Sequim Bay (48°2.3′N, 123°2.0′W), Iceberg Point (48°42.4′N 122°53.3′W), and Friday Harbor (48°54.5′N, 1230.7°W), all located in

[1] NMFS (National Marine Fisheries Service). 1998. Final environmental assessment and regulatory impact review for Amendment 36 to the Fishery Management Plan for the groundfish fishery of the Bering Sea and Aleutian Islands Area and Amendment 39 to the Fishery Management Plan for groundfish of the Gulf of Alaska to create and manage a forage fish species category, 76 p. NOAA/NMFS Alaska Regional Office PO Box 21668 Juneau, Alaska 99802-1668.

[2] Froese, R., and D. Pauly (eds.). 2004. Fishbase. World wide web electronic publication http://www.fishbase.org [accessed November 2004].

[3] Wang, J. C. S. 1986. Fishes of the Sacramento-San Joaquin estuary and adjacent waters, California: a guide to the early life histories, 602 p. Technical Report 9 of the Interagency ecological study program for the Sacramento-San Joaquin Estuary. [Available from Ecological Analysts, Inc. 2150 John Glen Drive, Concord, CA 94520.]

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Puget Sound, WA, and from adjacent waters. Specimens were initially preserved in 3.5% buffered formalin solution and later transferred to 70% ethanol (Busby et al., 2000). A dissecting stereomicroscope was used to examine pigmentation, general body size and structure, and to obtain meristic counts. Morphological measurements were made on 55 suitable specimens by using a digital image analysis system consisting of a video camera attached to a dissecting stereomicroscope and a computer with image analysis software. All measurements were taken from the left side of the specimen. Standard length was used throughout the study unless otherwise indicated. During flexion stage, notochord length (NL) was measured and recorded as SL. Measurements included standard length, head length, eye diameter, body depth, snout to anus length, and pectoral-fin length, as described by Moser (1996).

To describe osteological development of *A. flavidus*, with emphasis on the development of the caudal skeleton, 12 specimens were cleared and stained by using the technique described by Potthoff (1984). The terms "unossified precursor" or "element" are used to describe unossified elements that took up alcian blue stain but not alizarin red-s stain. From the cleared and stained specimens, stages of larval development were identified from landmarks of caudal-fin development. Caudal skeletons of six specimens representing distinct stages were used to create illustrations. Developmental stage terms follow Kendall et al. (1984) and Neira et al. (1998). The flexion stage was divided into three additional stages: early-, mid- and late-flexion. Early-flexion begins at hatching, mid-flexion begins with the formation of the forth hypural and epurals, and late flexion begins with the development of the fifth hypural and ends with complete notochord flexion. Nomenclature of caudal skeleton elements follows Fujita (1989).

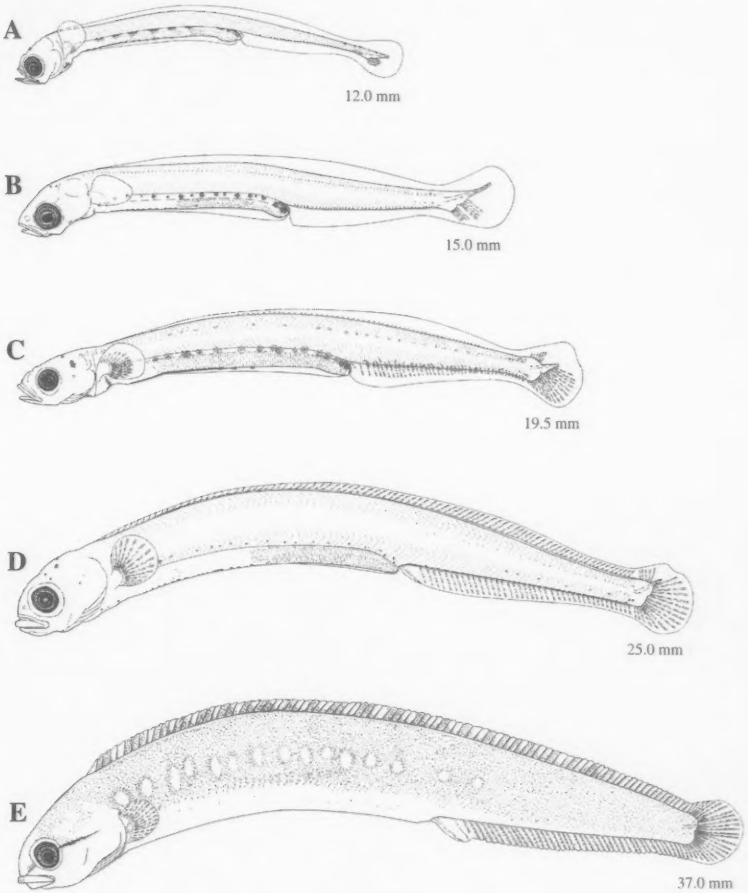

Figure 1

Developmental series of penpoint gunnel (*Apodichthys flavidus*).(**A**) Early-flexion larva, Clam Bay, 6 April 1989 (UW 104928); (**B**) mid-flexion larva (from Matarese et al., 1989); (**C**) late-flexion larva, Friday Harbor, 20 April 1994 (UW 104930); (**D**) postflexion larva, Clam Bay, 20 April 1989 (UW 104932); (**E**) juvenile, Sequim Bay, 25 April 1989 (UW 104934). Illustrations by Beverly Vinter.

Results

Morphology

Apodichthys flavidus larvae are approximately 12.0–13.0 mm at hatching and in early flexion stage and have little or no yolk sac present (Fig. 1A). The early-flexion stage occurs between hatching and 14.0 mm. Mid-flexion begins at approximately 14.0 mm (Fig. 1B), late-flexion at 17.0 mm (Fig. 1C), and postflexion at 20.0 mm (Fig. 1D). Transformation to the juvenile stage occurs between 25.0 mm and 30.0 mm. Juveniles examined ranged from 30.1 to 42.3 mm and looked like small

Table 1

Body proportions of larval and early juvenile penpoint gunnel (*Apodichthys flavidus*). Values given for each body proportion are expressed as percentages of standard length (SL) or head length (HL): mean ± standard deviation, and range.

Sample size, standard length, and body proportion	Flexion	Postflexion	Juvenile
Sample size	33	18	4
Standard length (SL)	14.9 ±2.1 (11.9–19.2)	21.9 ±1.3 (20.0–24.0)	34.2 ±5.6 (30.1–42.3)
Snout to anus length/SL	62.9 ±1.8 (58.0–66.1)	63.3 ±1.2 (61.8–66.1)	63.5 ±1.8 (62.5–65.2)
Body depth/SL	8.3 ±0.9 (6.4–9.9)	9.3 ±0.7 (8.2–10.4)	11.6 ±1.1 (11.2–12.9)
Head length/SL	13.2 ±0.7 (12.1–14.8)	14.1 ±0.7 (12.9–15.5)	16.4 ±1.1 (15.3–17.3)
Eye diameter/HL	33.6 ±4.7 (22.3–44.1)	27.4 ±3.1 (23.5–35.4)	20.0 ±3.9 (15.8–24.8)
Pectoral fin length/SL	7.6 ±1.2 (5.4–10.2)	7.9 ±1.0 (6.2–10.1)	6.2 ±1.4 (4.9–7.1)

adults (Fig. 1E). Larvae are slender bodied throughout development and body depth increases from 8% SL during flexion to 12% SL in juveniles (Tables 1 and 2). Head, snout-to-anus, and pectoral-fin lengths are consistent throughout development at approximately 14%, 63%, and 7% SL, respectively. Eye diameter decreases from 34% head length (HL) in flexion larvae to 20% HL in juveniles.

Pigmentation

Early-flexion larvae have a few faint melanophores located dorsally on the head and nape and a single melanophore on the isthmus (Fig. 1A). Along the dorsal surface of the gut, a row of large melanophores is present—irregularly spaced anteriorly and posteriorly, regularly spaced medially. Another row of smaller, evenly spaced melanophores is present along the anterior ½ to ¾ length on the ventral surface of the gut. A row of postanal ventral melanophores (PVMs) extends from the anus to the caudal peduncle. Generally there is one PVM per myomere but in many individuals one or more are missing from the row. In addition, there are small patches of melanophores along the dorsal and ventral margins of the caudal peduncle. In mid-flexion larvae, patches of melanophores on the head, nape, isthmus, and caudal peduncle are more defined, and a row of internal melanophores is present above the notochord (Fig. 1B). These melanophores develop simultaneously. In addition, the number of melanophores along the dorsal surface of the gut nearly doubles. The PVMs in late-flexion larvae are larger and more slashlike (Fig. 1C). During postflexion, pigmentation previously noted now appears very faint (Fig. 1D). Juvenile pigmentation resembles that of adults (Fig. 1E). Most notably, a horizontal streak of melanophores extends from the snout to the anterior margins of the eye and continues from the posterior margin of the eye to the mid-operculum. The body in live specimens is a uniform bright green to olive and has white spots located above the gut and anterior portion of the anal fin. The gut is generally unpigmented, with the exception of a few very small irregularly spaced melanophores on the lateral surface.

Osteology

Head region In early-flexion larvae the maxilla, mandible, two mandibular teeth, branchiostegal rays, and cleithrum are ossified. The premaxilla ossifies during mid-flexion. The remaining bones in the head region are not ossified until the juvenile stage.

Fins Unossified precursors of five principal caudal-fin rays are present at hatching and throughout early flexion. During mid-flexion, 12 unossified precursors of pectoral-fin rays and 13 unossified caudal-fin elements are present, both first appearing at 15.0 mm. Also at this size, a few faint unossified anal-fin elements are present in the anterior portion of the anal finfold, which are not visible in unstained specimens. Beginning at 17.0 mm, unossified precursors of dorsal-fin spines are first present in the area of the dorsal finfold above vertebrae 45–50 and then develop anteriorly and posteriorly from this position. Unossified anal-fin elements are also added from anterior to posterior. In addition, the scapula, coracoid, and radials of the pectoral fin are ossified and the adult complement caudal-fin elements is present, but still unossified (13 principal rays and 11 procurrent rays). By the end of late flexion (about 20.0 mm), elements of the dorsal, anal, and pectoral fins finally become ossified (Table 2). The single spine is the first element in the anal fin to become ossified. Pterygiophores of all fins are ossified in juveniles and the pectoral- and caudal-fin rays become ossified and branched. The number of fin elements present at any particular stage and length is somewhat variable as we noted slight differences in the numbers present between our stained and illustrated specimens.

Vertebral column At hatching, all neural and haemal spines are present and ossified (Table 2). In addition, vertebral centra begin to differentiate from anterior to

posterior during the early- and mid-flexion stages. At 17.0 mm, the vertebral centra are completely differentiated but remain unossified. In juveniles, the vertebral centra are completely ossified.

Caudal skeleton In early flexion larvae, the notochord begins to bend upward and the haemal spine of the second preural centrum, the fused parhypural plus first and second hypurals, and the third hypural are present (Fig. 2A). Caudal skeleton elements begin to ossify at this stage, beginning at the base of each. Ventral elements that develop at mid-flexion are the haemal spine of the third preural centrum and the fourth hypural (Fig. 2B). Dorsally, epurals 1–3 and neural spines of the second and third preural centra form during this stage. Elements present in early-flexion are now fully ossified. At the beginning of late-flexion (about 17.0 mm), a fifth hypural and a fourth epural are present but not ossified (Fig. 2C). In the 19.2-mm late-flexion specimen examined, the third and fourth epurals were fused and the first epural was fused to the neural spine of the second preural centrum (Fig. 2D). In postflexion larvae, the distal margins of hypurals 3–5 are oriented vertically and the first epural separates from the neural spine of the second preural centra (Fig. 2E). All other elements in the caudal skeleton have grown and are fully ossified. In juveniles, the caudal fin has the adult form and the final element, the uroneural, is present just ventral to the second and fused third and fourth epurals (Fig. 2F). A ventral caudal radial, present from mid-flexion to postflexion (Figs. 2, C–E), is absent in juveniles.

Discussion

Our description of *A. flavidus* development can be used to distinguish larvae of this species from co-occurring species of *Pholis* spp., *Apodichthys*, *Ulvicola*, and *Xererpes* along the West Coast of the United States. As with *Ulvicola sanctaerosae*, *A. flavidus* does not have a preflexion stage and larvae hatch at an advanced developmental state (Watson, 1996). Larval *Pholis* spp. differ from larval *A. flavidus* by the presence of pelvic fins in the former and by differences in pigmentation. The melanophores along the dorsal surface of the gut in *Pholis* spp. are more numerous (about 25 vs. about 18 in postflexion larvae) and closer in spacing anteriorly (Matarese et al., 1989), and *Pholis* spp. do not develop an internal row of melanophores along the dorsal margin of the notochord. *Apodichthys flavidus* develops a series of internal melanophores along the entire length of the notochord by the mid-flexion stage. Larvae of *U. sanctaerosae* can be distinguished from *A. flavidus* by pigmentation and by the number and persistence of pectoral-fin rays in postflexion larvae and juveniles. Larval *U. sanctaerosae* have fainter melanophores that are more irregularly spaced along the dorsal

Table 2

Meristics of cleared and stained larval and early juvenile penpoint gunnel (*Apodichthys flavidus*). Counts are of ossified elements only. Specimens above dashed line (- - - -) were undergoing notochord flexion.

Standard length (mm)	Dorsal-fin spines	Anal-fin elements	Pectoral -fin rays	Branchiostegal rays	Neural spines			Haemal spines	Centra			Caudal-fin rays
					abdominal	caudal	total		abdominal	caudal	total	
12.2				5	50	43	93	44				
12.8				5	50	42	92	43				
13.4				5	51	45	96	44				
14.6				5	52	43	95	42				
15.0				5	51	43	94	44				
17.0				5	52	42	94	45				
19.2	XC	I	15	5	50	41	91	44				
- - - -	- - - -	- - - -	- - - -	- - - -	- - - -	- - - -	- - - -	- - - -	- - - -	- - - -	- - - -	- - - -
21.2	XCI	I	15	5	50	43	93	45				
23.5	XCI	I	15	5	51	44	95	45				
30.1	XCII	I, 39	14	5	51	42	93	45	51	45	96	24
33.2	XCI	I, 41	15	5	50	43	93	43	50	45	95	24
42.3	XCI	I, 40	15	5	50	42	92	42	50	44	94	24

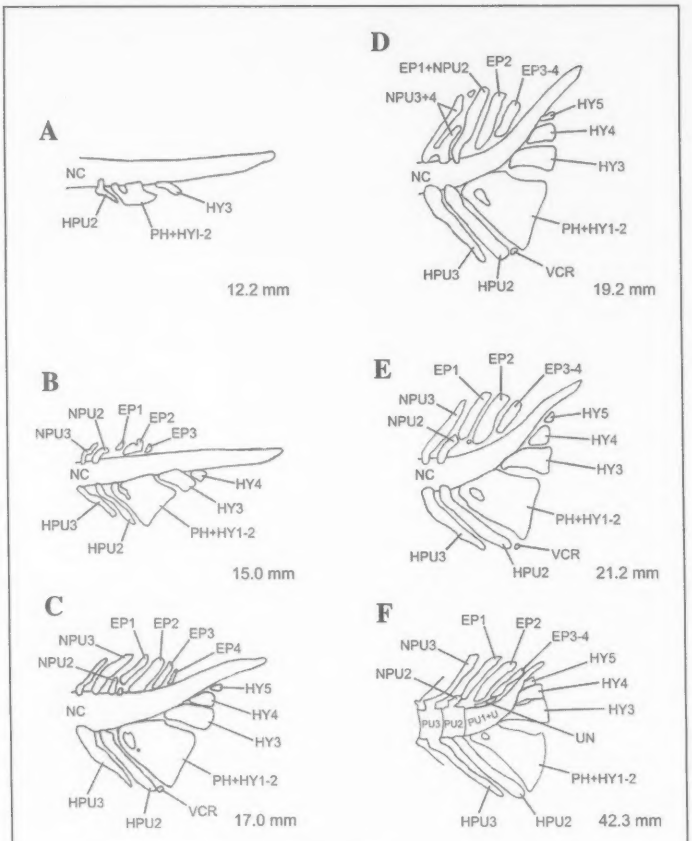

Figure 2

Caudal skeleton development of penpoint gunnel (*Apodichthys flavidus*). (**A**) Early-flexion larva, Clam Bay, 27 February 1995 (UW 104943); (**B**) mid-flexion larva (note irregularly shaped EP2), Clam Bay, 10 May 1989 (UW 104937); (**C**) late-flexion larva, Clam Bay, 19 April 1988 (UW 104939); (**D**) late-flexion larva, Clam Bay, 15 May 1989 (UW 104940); (**E**) postflexion larva, Friday Harbor, 8 April 1993 (UW 104943); (**F**) juvenile, Iceberg Point, 18 July 1963 (UW 018016). Caudal-fin element abbreviations: EP=epural; HPU=haemal spine, preural; HY=hypural; NC=notochord; NPU=neural spine, preural; PH=parhypural; PU=preural centra; U=urostyle; UN=uroneural; VCR=ventral caudal radial. Illustrations by Lisa De Forest.

surface of the gut than in *A. flavidus*, and in early- and mid-flexion larvae, these melanophores are restricted to the posterior ¼ to ½ of the gut. Another distinguishing characteristic is that *U. sanctaerosae* does not fully develop pectoral-fin rays and the pectoral fin does not persist after the juvenile stage. A pectoral finfold is present during the larval stage of this species; however, only the uppermost pectoral-fin rays (6 or 7 vs. 14 or 15 for *A. flavidus*) partially develop but do not persist, and the pectoral finfold decreases in size during the latter part of development. Larvae of *Xererpes fucorum* can be distinguished from *A. flavidus* by the presence of a preflexion stage and by having fewer total (84–93 vs. 96–101) and postanal (35–40 vs. 47–52) myomeres. In addition, during the later stages of development, *X. fucorum* has fewer pectoral-fin rays than *A. flavidus* (12 vs. 14–15).

Yatsu's (1985) revision of the family Pholidae placed *U. sanctaerosae* and *X. fucorum* in the genus *Apodichthys*, but this classification was not followed by Matarese et al. (1989), Watson (1996), or in the present study. Larvae of both these species are quite similar

to *A. flavidus*; however, we recommend a more detailed study of larval *U. sanctaerosae* and *X. fucorum*, including a description of caudal skeleton development, before concluding that larval characters do, or do not, support Yatsu's (1985) classification. In particular, it would be interesting to investigate whether either species develops a fourth epural that fuses with the third, or a first epural that fuses with the neural spine of the second preural centrum during flexion. In another cleared and stained individual we observed fusion of the neural spines on the third and fourth preural centra (NPU4 and NPU3, Fig. 3D). However, only one specimen of *A. flavidus* was examined at each of these fusions and more specimens, when available, should be cleared and stained to determine if these fusions occur in all larval *A. flavidus*. Presence or absence of a ventral caudal radial may also be of interest. Although it is unclear what becomes of the ventral caudal radial between postflexion and juvenile stages from our study of *A. flavidus*, we hypothesize that it fuses with the tip of the haemal spine of the second preural centrum. Taking all of these unusual aspects of *A. flavidus* larval development into account, we suggest that development of *U. sanctaerosae* and *X. fucorum* should be further investigated to clarify the systematic relationships among the genera.

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Spatial and temporal patterns in the bycatch of seabirds in the Argentinian longline fishery

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Longline fisheries have grown throughout the world's oceans for more than 40 years. This type of fisheries has captured high-quality fish (mature individuals rather than unwanted juveniles), has had minimal destructive effects on bottom habitats, and has produced a low bycatch of nontargeted fish (Brothers et al., 1999). Seabirds, however, are hooked accidentally when they swallow or are snagged on the baited hooks set by commercial longline crews (Brothers, 1991; Barnes et al., 1997; Tasker et al., 2000; Belda and Sanchez 2001; Jahncke et al., 2001).

Population declines of several species of albatrosses and petrels in the Southern Ocean are linked to longlining operations (Croxall and Prince, 1990; Brothers, 1991; Cherel et al., 1996). The importance of the Patagonian shelf waters as a foraging habitat for seabirds is well documented (Cooke and Mills, 1972; Veit, 1995), particularly for black-browed albatross (*Thalassarche melanophris*; Gales, 1998). We estimated the magnitude of seabird mortality in the kingclip (*Genypterus blacodes*) fishery in the Argentine Exclusive Economic Zone (EEZ).

Materials and methods

Description of the fishery

Demersal longline vessels target two species on the Patagonian shelf of Argentina: kingclip and Patagonian toothfish (*Dissostichus eleginoides*). Six vessels operate within Argentina's EEZ in the South Atlantic: three vessels, *Marunaka, Estela,* and *Magallanes II*, fish mainly kingclip off Comodoro Rivadavia and Puerto Deseado and three vessels, *Antarctic I, II* and *III*, target Patagonian toothfish off Ushuaia. Another twelve vessels based in the Malvinas (Falkland) Islands and operating outside Argentina's jurisdiction target kingclip and Patagonian toothfish (Blake, 2001; Fig. 1). Within Argentina's EEZ, an artisanal longline fleet of 70 vessels target hake (*Merluccius hubbsi*), fishing mainly in shallower waters within the San Matias Gulf.

The kingclip fishery operates year round with trips lasting up to 65 days. Vessels are equipped with an autoline system; the line is 10 km in length and has up to 20,000 hooks which are baited with thawed squid at night by using a baiting machine. Offal is released strategically to attract birds to the opposite side of the vessel away from the main line during hauling.

Data collection

Observers, trained in seabird identification and in quantifying mortality, estimated fishing effort and the bycatch of seabirds. Data were collected through a special agreement between a fishing company (Argenova S.A.) and the university (Universidad Nacional de la Patagonia Austral). Observers sampled 156 sets and hauls from December 2000 to September 2001. Sets were deployed as early as 23:00 and as late as 04:00. Observers recorded the date, number of hooks deployed, position and time of the start and end of each set, water depth, and sea condition. If a bird was caught, or if we observed flapping wings or the struggle of a bird, we recorded the event. During hauling we identified and counted all drowned birds. We collected a sample of drowned birds and brought them to the laboratory to determine their sex. Observers sampled the sets of one of the three vessels targeting kingclip in Argentina's EEZ. We estimated total bird catch using observed bycatch and official information, such us the number of hooks deployed from logsheets of the other vessels.

Data analysis

We used the bootstrapping method to calculate the 95% confidence limits for the mean number of birds caught/1000 hooks and made 10,000 simulations (n=156). Using logistic regression, we determined which variables best explained the "capture events." Initial independent variables included date, number of hooks deployed, water depth, latitude, sea condition, time at which the setting began, and moon phase. Moon phase was scored from 0 to 14, where 0 represents a full moon and 14, a new moon. To determine the contribution of each variable to seabird mortality rates, we used a stepwise multiple regression (Zar, 1984). On sets with catch per unit of effort (CPUE) greater than 0, three separate multiple regressions were performed: 1) for total seabirds, 2) for albatrosses, and 3) for petrels. Seabirds whose sex was determined were used to test differences from the 1:1 sex ratio by using a χ^2 test (Zar, 1984). We compared, using this test, the number of birds of each species caught during winter, summer and autumn (Zar, 1984).

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Results

Bycatch of fish and seabirds

The mean depth for longlining operations was 139 ±11 meters (n=156) and the mean number of hooks per set was 20,474 ±2588 (n=156). Effort for the whole fleet during the nine-month sampling period represented a total of 10,088,235 hooks.

Kingclip represented 80% of the fish caught. Additional catch included Patagonian toothfish (2%), Argentine hake (3%; *Merluccius hubbsi*), Brazilian codling (8%; *Urophycis brasiliensis*), blackbelly rosefish (2%; *Helicolenus dactylopterus lahillei*), skates (5%; *Raja* spp.) and other fish in proportions below 1% (i.e., Patagonian cod (*Salilota australis*); hoki (*Macrorunus magellanicus*); tope shark (*Galeorhinus galena*), Patagonian smoothhound (*Mustelus schmitti*), among others).

Only two species of seabirds were caught during setting of the longline: 12 white-chinned petrels (*Procellaria aequinoctialis*) and 19 black-browed albatrosses; no seabirds were caught during hauling. Most fishing and bycatch occurred between 48–46°S latitude and 63–61°W longitude (Fig. 1). The observed distribution of genders was not significantly different from an expected 1:1 sex ratio for albatrosses (χ^2=0.06, df=1), or petrels (χ^2=0.15, df =1). Fifty-three percent of the albatrosses caught were males and 47% females (n=17). White-chinned petrel were evenly divided: 50% were males and 50% females (n=12). Bycatch was not homogenous throughout the year. The majority of the petrels were caught during autumn (χ^2=66.3, df=2, P<0.001), whereas albatrosses were predominantly caught during winter (χ^2=54.7, df=2, P>0.001, Fig. 2). We estimated a mean bycatch rate of 0.034 ±0.009 birds/1000 hooks which, extrapolated to the other vessels, represents a total of 343 birds caught in a nine-month period. Of these birds, 55% would be black-browed albatross and 45% white-chinned petrels.

Figure 1

Map showing ports (solid triangles) used by longliners in Argentina. Open triangles indicate set positions where seabird bycatch occurred and circles indicate sets without seabird bycatch. The 200-m isobath indicates the shelf break.

Factors affecting bycatch rates

Logistic regression analysis indicated that water depth (β_0=−0.96) and moon phase (β_0=0.24) explained most of the variability in "capture events"; the probability of a bird getting caught increased with water depth and during brighter nights. Two variables were important in explaining the variation in bycatch rate (F=3.13; df=4, 42; P=0.02): moon phase (β=−0.327, P=0.03) and water depth (β=0.335, P=0.02). When we analyzed the variables that explained the incidental capture for both species separately, moonlight was the most important for albatrosses (F=4.637, df=3, 21, β=−0.52, P<0.01), whereas water depth was the most important for petrels (F=2.4, df=2, 22, β=0.584, P<0.05).

Discussion

This note reports the first estimation of seabird bycatch in the Argentinean EEZ outside of the CCMLAR (Commission for the Conservation of Antarctic Marine Living Resources) area for the Atlantic Ocean with data from onboard observers. Pelagic seabird species, such as white-chinned petrels and black-browed albatrosses, actively forage in the highly productive Patagonian shelf waters (Cherel and Klages, 1998; Prince et al., 1998; Weimerskirch et al., 1999; Grémillet et al., 2000); therefore these species are especially vulnerable to fisheries around coastal shelf-edge habitats (Weimerskirch et al., 1999; Grémillet et al., 2000). These two species are often associated (Veit, 1995) and are similarly affected by longline fishing (Moreno et al., 1996; Berrow et al., 2000). We found the average bycatch rate to be 0.034 birds/1000 hooks, which is one or two orders of magnitude lower than those reported from other longline

fisheries in the South Atlantic (i.e., Brazil 0.126 birds/1000 hooks; [Neves and Olmos, 1998], Uruguay 4.7 birds/1000 hooks; [Stagi et al., 1998]), but similar to those reported for the CCAMLR region (1998: 0.025 birds/1000 hooks; 1999: 0.07 birds/1000 hooks; 2000: 0.0014 birds/1000 hooks; [Robertson et al., 2001]).

We made bycatch estimations from vessels, while voluntarily using mitigation measures to reduce fishery-induced mortality on seabirds—such as tossing thawed bait (less bouyant than frozen bait), setting lines only at night, and splashing the net buoys when birds came near the line. In a nine-month period, 343 seabirds were incidentally caught by vessels targeting kingclip, representing an annual mortality estimate of 457 birds. Previous crude estimations made for day-setting were considerably higher (2 birds/1000 hooks, Gandini and Frere, 2001).

The main factor affecting seabird mortality was water depth, which is directly related to the location of the setting because water depth increases towards the shelf break, where white-chinned petrels forage actively throughout the year (Weimerskirch et al., 1999; Berrow et al., 2000). Sixty-five percent of the birds were caught between five days after or before the full moon. A full moon affected albatrossess more significantly than it did petrels. Albatrosses forage mainly during the day, whereas white-chinned petrels forage both at night and during the day (Weimerskirch et al., 1999). Our results support the theory that darkness reduces seabird bycatch. Therefore, improving mitigation measures (i.e., using streamer lines, splashing bouys, etc.), during full moon phases, may reduce bird bycatch further. Birds were more susceptible to being caught in autumm and winter. Our findings agree with those of White et al. (2001), who mentioned that vulnerability for seabirds in Patagonian shelf waters is higher between September and June than during the rest of the year.

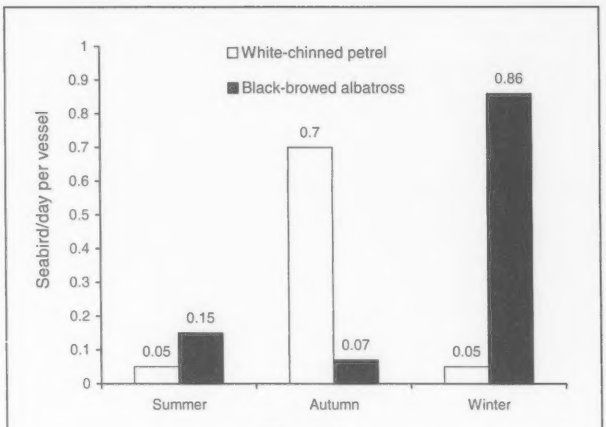

Figure 2

Bycatch rates for black-browed albatross *(Thalassarche melanophris)* and white-chinned petrels *(Procellaria aequinoctialis)* incidentally killed in longline fishery operations in Argentinian waters.

Population impacts and recommendations to reduce bycatch of seabirds

At least 500,000 pairs (nearly 86% of the world population) of black-browed albatrosses breed on the Malvinas and Falkland Islands and forage on the highly productive Patagonian shelf. Thus, the black-browed albatross catch estimated in this study represents <1% of the total population. Similarly, the world population of white-chinned petrels is estimated at more than a millon breeding pairs (Croxall et al., 1984; Woods and Woods, 1997); therefore, less than 1% of the white-chinned petrel population is removed by longlining each year. Although these estimates may not seem to be critical for the affected species, they may be more significant than indicated because even a small increase in long-lived species may cause populations to decline. Moreover, the lack of information on seabird bycatch by illegal, unreported, and unregulated fishing, make the overall population-level impact from bycatch not only difficult to assess but likely much higher than currently realized. Estimations of seabird bycatch by illegal fleets range from 7000–15,000 albatrosses and 1200–2000 petrels killed during 2000 (Baird, 2001). These figures are almost seven times larger than our estimates for the Argentinian kingclip fleet operating in the south Atlantic.

Our data indicate that collaboration between fisherman and technicians to find devices that reduce bait loss and that improve fish CPUE for practical application (no additional actions to be taken during fisheries operations) is likely critical to maintaining seabird populations. We recommend offering financial benefits to fishing crews that catch fewer seabirds and offering appropriate fishing gear and incentives for compliance in order to reduce seabird bycatch in the Atlantic Ocean.

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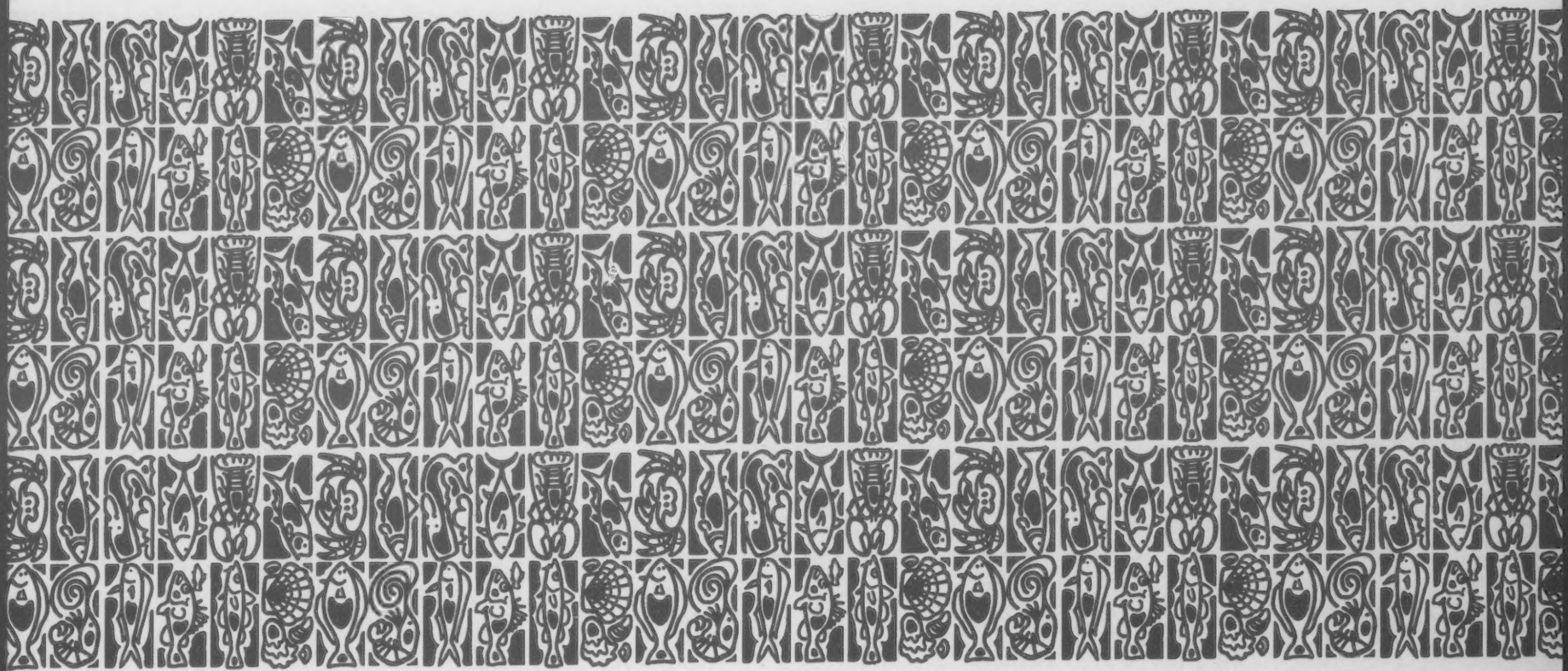
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